Appendix B

The Use of Conceptual Ecological Models to Guide Ecosystem Restoration in South Florida (Ogden 2005)

A Conceptual Ecological Model of Florida Bay (Rudnick 2005)

A Conceptual Model of Ecological Interactions in the Mangrove Estuaries of the Florida Everglades (Davis 2005)

WETLANDS, Vol. 25, No. 4, December 2005, pp. 795–809

THE USE OF CONCEPTUAL ECOLOGICAL MODELS TO GUIDE ECOSYSTEM RESTORATION IN SOUTH FLORIDA

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Abstract: Conceptual ecological models, as used in the Everglades restoration program, are non-quantitative planning tools that identify the major anthropogenic drivers and stressors on natural systems, the ecological effects of these stressors, and the best biological attributes or indicators of these ecological responses. Conceptual ecological models can be used with any ecological restoration and conservation program and can become the primary communication, planning, and assessment link among scientists and policy-makers. A set of conceptual ecological models has been developed for South Florida restoration as a framework for supporting integration of science and policy and are key components of an Adaptive Management Program being developed for the Comprehensive Everglades Restoration Plan. Other large-scale restoration programs also use conceptual ecological models. This special edition of Wetlands presents 11 South Florida regional models, one total system model for South Florida, and one international regional model. This paper provides an overview of these models and defines conceptual ecological model components. It also provides a brief history of South Florida's natural systems and summarizes components common to many of the regional models.

Key Words: South Florida, Everglades, ecosystem restoration, conceptual ecological models, applied science strategy, adaptive management, sea-level rise, water management, urban development, agricultural development

INTRODUCTION

The rapid expansion of human impacts on entire natural ecosystems, and the resulting increasing scales of degradation of these environments, has created new challenges for the natural resource managers who are responsible for protecting and restoring the wild lands of the United States. Chesapeake Bay's waters are greatly degraded, Louisiana's coastline is receding into the Gulf of Mexico, and the Florida Everglades are both hydrologically altered and spatially fragmented. Programs designed to reverse these undesirable trends require integration of science and policy at scales not previously attempted in order to establish agreement on restoration objectives as the basis for restoration planning and to create the foundation for experimentation and monitoring for adaptive management. The challenge of organizing and applying good scientific understandings is especially great given the large spatial and temporal scales at which regional ecosystems operate and at which restoration plans must be designed and implemented to resolve these issues. Yet, current understanding of large, regional ecosystems is often substantially incomplete, and existing knowledge is widely scattered in place and time (and all too often unpublished). Despite these challenges, resource agencies and institutions must move forward with planning and implementing complex restoration programs before further degradation occurs. The need is for a logical process for synthesizing, organizing, and prioritizing existing knowledge of these ecosystems as a basis for maximizing an effective role for science in supporting the planning and assessment of regional restoration programs.

Since 1995, teams that have been planning and implementing restoration programs in South Florida have developed a set of non-quantitative conceptual ecological models as a framework for supporting this integration of science and policy. These conceptual models identify where there is broad agreement about major anthropogenic stressors on natural systems, ecological effects of these stressors, and best biological attributes or indicators of these ecological responses. In short, the models provide qualitative explanations of how natural systems have been altered by human stressors, which in turn provides planners with the information needed to focus on the best design and assessment strategy for the regional restoration program. In South Florida, these models have become powerful tools for developing consensus and communicating prevalent views of the major "working hypotheses" that explain what we know and don't know about the stressor linkages and effects in the greater Everglades basin, as a basis for developing an evolving set of performance measures, monitoring programs, and an adaptive management strategy for dealing with numerous uncertainties in ecosystem responses. It is important to emphasis that these conceptual models are non-quantitative, and have been designed primarily as planning tools for Everglades restoration. Secondarily, these models have contributed to discussions of research priorities in the context of the science needed to support Everglades restoration.

This initial paper describes the development and principal application of conceptual models. The following papers provide the scientific framework and underpinnings for 11 South Florida regional models, one total system model for South Florida, and one international regional model. Conceptual ecological models can be used with any ecological restoration and conservation program and, when developed and applied appropriately, can become the primary communication, planning, and assessment link among scientists and policy-makers.

HISTORY OF THE GREATER FLORIDA EVERGLADES ECOSYSTEM

South Florida was once a diverse mosaic of hydrologically interconnected landscapes and communities (Beard 1938, Davis 1943, Douglas 1947, Davis and Ogden 1994, Gunderson 1994, Browder and Ogden 1999). The expansive freshwater Everglades covered an area of about 1.2 million ha (Davis et al. 1994) and was the heart of a 3.6 million ha wetland system (Davis and Ogden 1994). The pre-drainage South Florida ecosystem has been characterized as a hydrologically interconnected, slow flowing system that extended from the Kissimmee River and Lake Okeechobee southward over low-gradient lands to the estuaries of Biscayne Bay, Ten Thousand Islands, and Florida Bay and eastward and westward to the northern estuaries (Figure 1). Excess water flowed overland to the Caloosahatchee Estuary and into the Gulf of Mexico, overland to the St. Lucie and Loxahatchee River Estuaries and Indian River and Lake Worth Lagoons into the Atlantic Ocean, and spilled over the low southern shore of Lake Okeechobee into the Everglades and south to Florida Bay (Obeysekera et al. 1999). Lake Okeechobee had no direct connection to the Atlantic Ocean or the Gulf of Mexico.

The South Florida natural ecosystem is the product of a unique combination of climate, soil, and topography (Obeysekera et al. 1999). Water depth and distribution, temporally and spatially, were largely determined by seasonal and annual rainfall, evaporation, transpiration, natural topography, outflow through natural streams into the ocean, and the system's capacity for surface- and ground-water storage (SFWMD 1992, Fennema et al. 1994). This large water-storage capacity resulted in a system much wetter, but not necessarily deeper, than the current system. Alternating high and low water depths and distribution patterns of surface water and ground water in the freshwater wetlands, as well as variations in water flow volumes and rates through wetlands and into estuaries largely determined soil and vegetation patterns. Hydrology also determined the distribution, abundance, and seasonal movements and reproductive dynamics of all aquatic and many terrestrial animals in the Everglades (Powell 1987, Kushlan 1989, Davis and Ogden 1994, Fennema et al. 1994, Holling et al. 1994, Walters and Gunderson 1994). The effects of this slow-moving sheet of water, in concert with natural climatic events such as fires, freezes, storms, hurricanes, floods, droughts, and sea-level change (Craighead 1964, Wanless et al. 1994, Browder and Ogden 1999) created and sustained a mosaic of ponds, marshes, hardwood hammocks, and forested wetlands. Local topographic and substrate differences were responsible for fine-scale vegetation patterns (Browder and Ogden 1999). The large spatial extent and connectivity of the Everglades were essential for sustaining populations of species with narrow habitat requirements or large feeding ranges and sustaining regional levels of aquatic production necessary to support large numbers of higher vertebrates (Harshberger 1914, Harper 1927, Ogden et al. 1999).

South Florida's rapidly increasing population has impacted the South Florida ecosystem. By the late 1990s, almost 6 million people were living along the coast of South Florida (Gannon 1996). Given the large numbers of people living in former low-lying wetlands, water management has been a constant and necessary practice for South Florida. Land was drained for urban and agricultural development, and canals and conservation areas were constructed for flood control, water retention, water supply, irrigation, and transport. South Florida now contains one of the largest water-management systems in the world, the Central and Southern Florida (C&SF) Project (USACE 1960, Light and Dineen 1994, USACE 1998) that was authorized by the US Congress in 1948 and constructed during the 1950s–1970s. This infrastructure was designed for a projected population of only 2 million people in

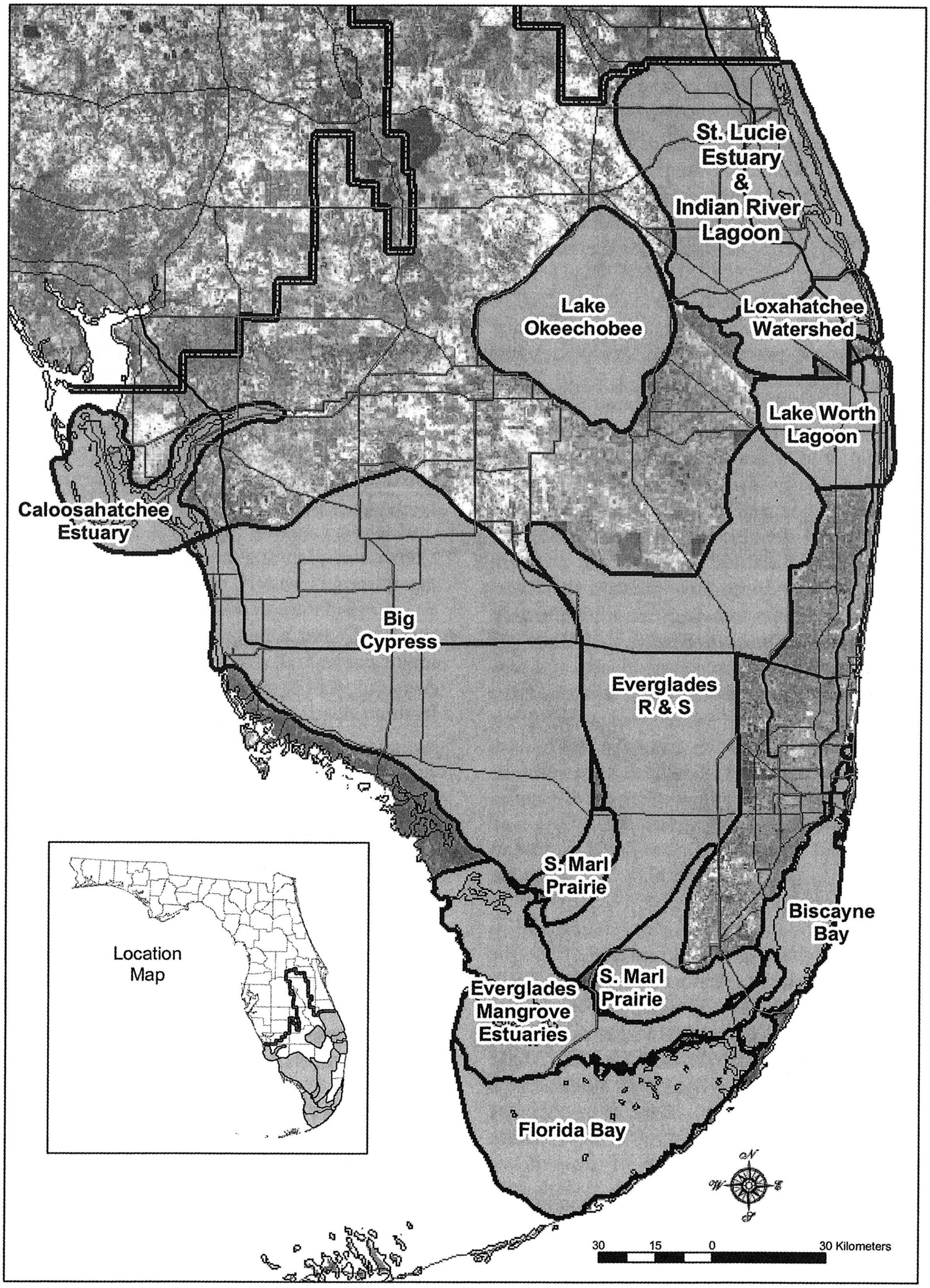

Figure 1. Map of South Florida with conceptual ecological model boundaries.

2000 (USACE and SFWMD 2004). Population in South Florida is now projected to increase to 8–15 million people by 2050 (USACE 1998, Harwell et al. 1999, National Park Service 2000, US Army Corp of Engineers 2003).

At present, approximately one-third of the original extent of the greater wetland system in South Florida has been lost or converted to other land uses, including about one-half of the true Everglades (Tebeau 1990, Chapman 1991, Davis et al. 1994, Harwell et al. 1996, Harwell 1997, Harwell 1998, M. Duever, South Florida Water Management District, pers. comm. 2002). Remaining wetlands have been increasingly impacted by water-management practices. The Everglades has lost 50% of its habitat, and 70% less water flows through the system (USFWS 1999). Around 6.4 billion kilograms of water are lost into the ocean every day for flood control, and water demand for human consumption increases daily. Large flood control releases from Lake Okeechobee and major canals during the wet season and water demand withdrawals during the dry season have altered habitat conditions in northern estuaries. Disruption of sheet flow through the Everglades has reduced the amount of fresh water flowing into southern estuaries. In both Florida and Biscayne Bays salinity levels have risen, water clarity and seagrass habitat have been reduced, algal blooms have occurred, and fish and invertebrate populations have decreased as fresh water flowing from the Everglades has decreased. Many hectares of habitat have been affected by phosphorous. Nesting wading bird population has been reduced 90–95% since the 1930s, and 68 plant and animal species are now listed as threatened or endangered, while nearly 600,000 hectares are being invaded by exotic species (USFWS 1999).

As a result of Everglades habitat degradation and an increasing human population, Congress authorized the Comprehensive Everglades Restoration Plan (CERP) in 2000 (USACE and SFWMD 1999, Water Resources Development Act of 2000) to assist in the restoration of South Florida's natural systems (SFERTF 2000). Estimated to cost $8.2 billion (in 1999 dollars), the project will span over thirty-five years. It may be the largest environmental restoration project ever authorized. The main restoration objectives of the plan are to increase water storage capacity of the system substantially and distribute water in a manner to reestablish ecologically desirable patterns of depth, distribution, and flow in freshwater wetlands and desirable salinity regimes in estuaries (Ogden et al. 2003). It is expected that these improvements in hydrologic patterns will result in substantial improvements in the system's ecological condition (Ogden et al. 2003). The plan specifies that it will be based on the ''best available science'' and the concept of ''adaptive assessment,'' which will allow the plan to be flexible so modifications can be made based on new information (Ogden et al. 2003). Modifications will be made as needed through the adaptive management process discussed below.

ROLE OF SCIENCE IN SUPPORTING EVERGLADES RESTORATION

Applied Science Strategy

An ''applied science strategy'' was developed in South Florida as a process for linking science and management during the planning and implementation of the South Florida ecosystem restoration programs (Ogden et al. 1997, Science Coordination Team 1997, Ogden and Davis 1999). The purpose of the strategy has been to organize and convert large amounts of existing scientific and technical information into planning and assessment tools that would support restoration. An organizing process is required for large-scale restoration planning because information from many disciplines is widely scattered in time and place, focused efforts are needed to include ''best professional opinion,'' and a large degree of consensus regarding major cause-and-effect relationships is necessary. Ogden et al. (2003) described the applied science strategy in more detail.

Role of Conceptual Ecological Models

The principle organizing component in the applied science strategy is a set of non-quantitative, conceptual ecological models of 11 major physiographic regions in South Florida. These conceptual models are being used as planning tools to guide and focus scientific support for the South Florida ecosystem restoration initiatives and to build understanding and consensus among scientists and managers regarding the set of working hypotheses that explain the sources and effects of major anthropogenically induced changes in the natural systems of South Florida. The hypotheses identify specific, large-scale stressors on the natural systems, ecological effects of these stressors, and recommended biological and ecological attributes of the natural systems that can best serve as indicators of the effectiveness of restoration programs designed to reduce or eliminate the effects of the identified stressors. In other words, each hypothesis describes ecological linkages between a stressor and a key attribute of the natural system that has been altered due to effects of that stressor.

Conceptual ecological models have become an essential part of South Florida's restoration planning process because both scientists and managers now depend on the models to help build scientific consensus regarding ecosystem linkages and responses, as a framework for creating performance measures used both to plan the design of the restoration programs and assess responses of the natural systems during implementation of each program, and to identify research needs. Managers appreciate these models because of their role in organizing effective application of existing science in support of decision-making during the restoration planning process. Scientists value the intellectual and integrative processes of developing working hypotheses and laying out linkages in conceptual models as a basis for identifying gaps in knowledge and setting research priorities. Specific hydrologic, water quality, biological, and ecological performance measures derived from stressors and attributes in the models (RECOVER 2004), in addition to focusing restoration planning on quantitative objectives, also define the content of system-wide monitoring programs designed to measure system responses to restoration efforts.

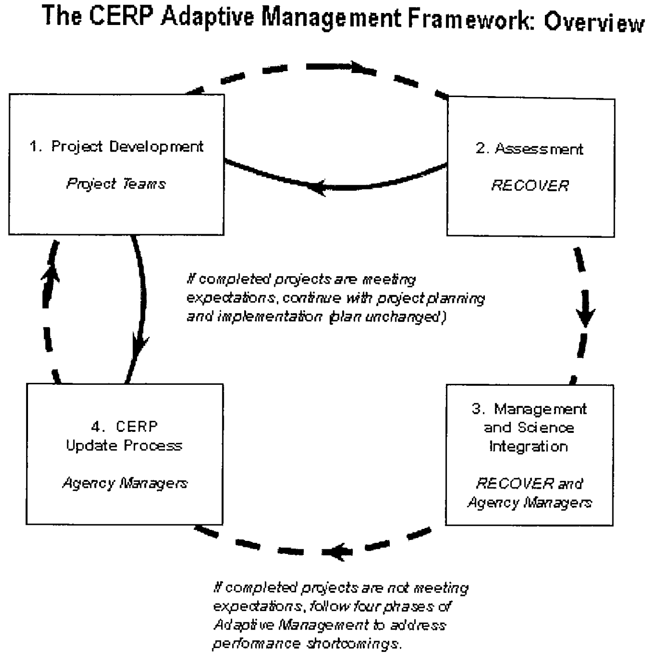

Figure 2. The CERP Adaptive Management Process.

Adaptive Management

Conceptual ecological models are key components of an Adaptive Management Program that is described in the Programmatic Regulations for the Comprehensive Everglades Restoration Plan (Department of Defense 2003). Adaptive management is a continuous process of seeking a better understanding of the interactions between the natural and human systems and refining and improving a restoration plan to respond to changes or unforeseen circumstances and new scientific and technical information.

The CERP Adaptive Management Program is currently being designed to anticipate future uncertainties and respond to system responses for success. These uncertainties include unanticipated and undesired responses and events in natural and human systems of South Florida that result from CERP implementation or from non-CERP influences, including external drivers in conceptual ecological models. A successful adaptive management program will provide early warnings of undesired impacts and allow decision-makers to integrate science and management effectively as a basis for providing on-going refinements in the plan to ensure that its goals are achieved.

A draft framework for the strategy to be used to implement adaptive management is presented in Figure 2. The conceptual ecological models, as the source for performance measures, serve tasks in Box 2: Performance Assessment. Performance assessments are based on information obtained through a system-wide monitoring program that focuses on physical and biological elements identified by assessment performance measures. Response of the system to restoration efforts is determined by applying monitoring data to performance measures and assessment protocols. Results of these analyses will determine what portions of the restoration plan are successful or not. Conceptual ecological models will be revised to the extent that monitoring and assessment activities result in improvements in our understanding of cause-and-effect relationships in the natural systems.

SUMMARY OF SOUTH FLORIDA CONCEPTUAL ECOLOGICAL MODELS

This paper introduces a Total Systems Model and eleven regional conceptual ecological models: 1) Everglades Ridge and Slough, 2) Everglades Southern Marl Prairies, 3) Everglades Mangrove Estuaries, 4) Big Cypress Regional Ecosystem, 5) Florida Bay, 6) Biscayne Bay, 7) Lake Okeechobee, 8) Caloosahatchee Estuary, 9) St. Lucie Estuary, 10) Loxahatchee Watershed, and 11) Lake Worth Lagoon (Figure 1).

Development of the Conceptual Ecological Models

Through workshops, participants identified causal hypotheses that best explain major anthropogenically-driven alterations in each landscape. Participants then created lists of appropriate stressors, ecological effects, and attributes (indicators) for each region. The objective was to identify physical and biological components and linkages in each landscape that best characterized changes explained by hypotheses. Each preparer (model lead) used hypotheses and lists of components to draft a model and prepare a supporting narrative to explain organization of the model and supporting science for hypotheses (RECOVER 2001, 2003).

In addition to the set of regional conceptual models developed, a Total System Model for South Florida has been created for several purposes beyond the scope of regional models. The Total System Model is used to identify working hypotheses that are relevant to all or a substantial subset of regional models, as a basis for determining stressors, ecological linkages, and attributes that are associated with the most important changes that have occurred over much of the natural areas of South Florida. Inclusion of working hypotheses at total system scales elevates the significance of these hypotheses in overall planning for restoration. The Total System Model also allows for a better characterization of stressors and ecological linkages that are operating at larger scales than can be presented adequately in regional models (e.g., altered nesting and foraging patterns by wading birds) and of altered hydrologic conditions having ecological effects across boundaries of adjacent regional models (e.g., altered nutrient and sediment transport between freshwater and estuarine regions). Unlike most regional models, the Total System Model includes consideration of working hypotheses that address changes that have occurred in upland landscapes in South Florida (e.g., pinelands).

SUMMARY OF THE INTERNATIONAL MODEL

Located on the Caribbean Coast in the state of Quintana Roo, the Sian Ka'an Reserve and South Florida, USA are remarkably similar. Valuable lessons in ecosystem ecology are being learned from the South Florida Ecosystem Restoration Initiative that can and should be applied to the Sian Ka'an Biosphere Reserve. The conceptual ecological model for the Sian Ka'an Reserve does not explain effects that have already occurred on ecological habitats and linkages between hypotheses but, rather, predicts effects that will occur due to current human pressures. The model predicts linkages allowing scientists to measure and protect precious attributes. The purpose of this conceptual ecological model is to identify important attributes and conditions required for their success. Sian Ka'an has the opportunity to test conceptual ecological models in a system that has not been extensively or intensively developed or degraded as South Florida ecosystems.

The Sian Ka'an Conceptual Ecological Model is analogous to the Everglades Total System model in scope and scale. The process for constructing the Sian Ka'an Biosphere Reserve model was modified slightly

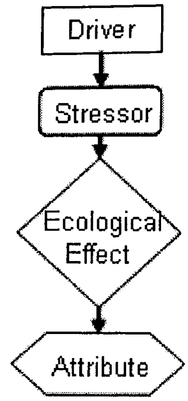

Figure 3. Simplified diagram of a conceptual ecological model.

from that of Everglades' conceptual ecological models. Drivers, stressors, attributes, and effects/linkages were initially identified from a series of local workshops with area experts, primarily from Amigos de Sian Ka'an (ASK) and the National Commission for Protected Natural Areas (CONANP) staff in November 1999 in Cancún.

MODEL COMPONENTS

The models include all major external drivers, stressors, ecological effects, and attributes that illustrate the major cause-and-effect linkages in each modeled region, regardless of their connection to the CERP. A schematic diagram of a conceptual ecological model is presented in Figure 3. Models depict general pathways by which driving forces (in rectangles) affect attributes of the ecosystem (in hexagons) that are important to ecosystem function and those viewed by people in south Florida as valuable and important to maintain. External drivers create internal stressors (ovals) that have various effects (diamonds) on the ecosystem, which are reflected in changes to ecosystem attributes (hexagons). To help illustrate the actual nature of the model components, examples of a working hypothesis as diagramed in a conceptual model are shown in Figure 4.

These major components of the models are defined as follows:

- Drivers—major driving forces that occur outside the natural system, which have large-scale influences on natural systems. Drivers are natural forces (e.g., sea-level rise) or anthropogenic (e.g., water management).
- Stressors—physical or chemical changes that occur within natural systems that are brought about by drivers, causing significant changes in biological

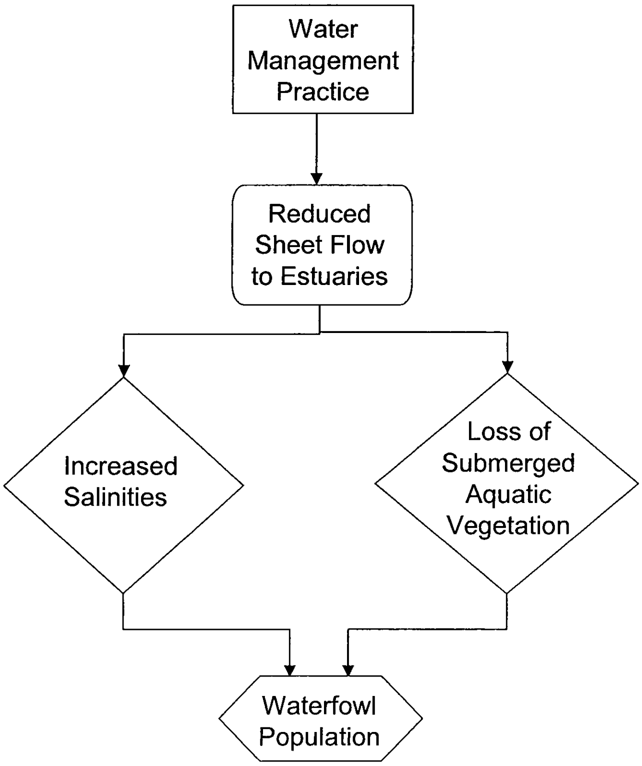

Figure 4. An example of an Everglades working hypothesis as diagramed in a conceptual model.

components, patterns and relationships in natural systems.

- Ecological Effects—physical, chemical, and biological responses caused by stressors.
- Attributes—a parsimonious subset of all potential biological elements or components of natural systems that are representative of overall ecological conditions of the system. Attributes typically are populations, species, guilds, communities, or processes. Attributes, also known as indicators or endpoints, are selected to represent known or hypothesized effects of stressors (e.g., nesting wading bird numbers) and elements of systems that have important human values (e.g., endangered species, sports fishing).

In the text for the models, attributes are discussed before ecological effects even though they are at the end of the pathway in the diagrams. Chapters are organized in this manner to provide the reader with background information on stressors and attributes prior to reading the discussion of ecological effects and critical linkages that are the basis for causal hypotheses.

As we learn more about how the ecosystem functions, it is possible that additional pathways could be added to the models or adjustments made to existing pathways. Models are flexible planning tools that, at any given time, reflect the current state of scientific knowledge about the regional or total system.

Although each regional model has a specific set of components, many key components overlap among models. Below is a generalized discussion of the more widespread drivers, stressors, and attributes that are common to most or all of the regional models. The information is presented here once, rather than repetitively within each regional model paper. Because ecological effects and critical linkages are more likely to vary among regional models, all effect discussions are retained in narratives for each model and are not summarized in the following general discussion.

Drivers

Each model lists or implies three major drivers: sea-level rise, water management, and urban and agricultural development. These drivers affect many attributes, but most frequently water quality, water levels, water patterns, water flow, toxin concentrations, habitat, and species composition.

Sea-Level Rise. There is strong evidence that present rates of sea-level rise in South Florida, which are attributed to global climate change, will massively reconfigure the geomorphology, circulation patterns, salinity patterns, and ecological processes during the Twenty-First Century (Wanless et al. 1994). The entire South Florida ecosystem is dependent on water flow and habitat area. Given that Florida is characterized by very small topographic relief, a conservatively estimated sea-level rise of 0.75 m over the next century (Wanless et al. 1994) will reduce shoreline habitat, overall habitat extent, and mix sediments and salinities altering water composition. Effects are further explained in the following attributes and linkages and within each model.

Water Management. Since the mid-1800s, water management has been designed to accommodate and support an influx of population. Water supply and flood control have been achieved by a complex system of structural and operational modifications to the natural system. Alterations affecting hydrology include construction of canals, channelization of natural waterways, filling, draining, and/or impoundment of wetlands, and creation of new inlets to the Atlantic Ocean. These modifications have 1) contributed to substantial reduction in spatial extent, 2) provided a network of canals and levees that have accelerated spread of degraded water and exotic species, 3) greatly reduced water storage capacity within remaining natural systems, 4) created an unnatural mosaic of impounded and overdrained marshes in the Water Conservation Areas, and 5) substantially disrupted natural patterns of sheet-flow direction, location, and volume (SFWMD 1992, Science Subgroup 1993, Davis and Ogden 1994, Fennema et al. 1994, Light and Dineen 1994). Declines in many ecological attributes correspond to development of the water management system.

Urban and Agricultural Development. Increasing population forced engineers to drain extensive areas of wetlands, both large and small, to provide space for development, provide flood protection, and to accommodate increasing urban and agricultural water demands. Clearing and paving of land prevents precipitation drainage and water-table replenishment.

Agricultural runoff contaminates water with nitrogen, phosphorus, pesticides, herbicides, and fungicides. Citrus farms, vegetable fields, cattle ranchers, and sugarcane fields now reside where flowing water once nourished native vegetation and animal species. This rapid, mass development resulted in fragmented habitats, degraded shoreline and coastal habitats, and contaminated water supplies.

Stressors

Stressors common to all or many of the models include altered hydrology, degraded water quality, reduced spatial extent, physical alterations, increases in exotic species, and boating and fishing pressure.

Altered Hydrology. Change in direction, volume, and timing of freshwater flow has altered hydrology in South Florida. Water-management practices for flood control and water supply have resulted in unnatural discharges of water to prevent flooding and water withdrawals for irrigation and consumption that reduce flow volumes during drought conditions. For inland models (Everglades Ridge and Slough, Southern Marl Prairies and Big Cypress Regional Ecosystem), altered hydrology takes the form of altered hydropatterns, especially altered hydroperiods (period of inundation). For Lake Okeechobee, lake stages are often too high or too low. Salinity regimes of all estuaries (Everglades Mangrove Estuaries, Caloosahatchee Estuary, St. Lucie and Indian River Lagoon, Loxahatchee Watershed, and Lake Worth Lagoon Conceptual Ecological Models) have been altered from changes in location, volume, and timing of fresh water.

The South Florida wetland ecosystems relied on a continuous and slow-moving sheet of water. Any interruption in that flow of water results in altered hydropatterns. Hydropattern includes depth, period of inundation, and sheet flow. Many species are dependent on specific hydropatterns, including fish, alligators (*Alligator mississippiensis* Daudin), benthic communities, submerged aquatic vegetation (SAV), and wading birds. With a shortened hydroperiod, the amount of water and duration of surface-water flooding in natural wetlands dramatically decreases, reducing the extent and quality of habitat and food supply for many species. Drier conditions can facilitate major shifts in the composition of affected wetland plant communities to a composition similar to upslope communities. An altered and less hospitable landscape allows for invasion of exotic species and a drier community opens the area up to more frequent and damaging fires.

Estuarine environments are sensitive to freshwater inputs. Modifications to natural patterns of volume, distribution, circulation, or timing of freshwater discharges can alter an estuary's salinity regime (Haunert et al. 1994). During the wet season, rainfall that was historically retained within the undeveloped watershed now reaches estuaries faster and in greater volume. During the dry season, less fresh water flows into estuaries, allowing encroachment of saltwater upstream. A heightened sea level will also continue to mix more saltwater with areas previously filled with fresh water, altering water quality and habitat conditions. The salinity regime of an estuary is a primary determinant of the species composition of communities, as well as strongly influencing functions of these communities (Kennish 1990, Sklar and Browder 1998). All estuarine biota have adapted to a given salinity range and a given degree of salinity variability. Rapid and unnatural fluctuations in salinity have contributed to major impacts on SAV abundance and distribution, productivity, community composition, predator-prey relationships, and food-web structure. It is a major factor limiting the distribution and abundance of alligators (Dunson and Mazzotti 1989, Mazzotti and Dunson 1989) and survival of juvenile crocodiles (*Crocodylus acutus* Cuvier) (Mazzotti et al. 1988, Mazzotti 1989, Mazzotti and Dunson 1989, Moler 1991).

Degraded Water Quality. Water quality throughout South Florida has been degraded by elevated nutrient loads, inputs of contaminants, and elevated suspended solids. Phosphorus increases can be traced back to application of fertilizers to urban and agricultural lands and processing of human and agricultural waste products, run off of which is facilitated by water-management practices (Drew and Schomer 1984, Post et al. 1999). Absence of adequate storage and treatment facilities requires delivering flood waters rapidly into wetlands and receiving water bodies with little potential for amelioration of nutrient and dissolved organic matter loads. High peak flow rates also scour canal bottoms and erode canal banks, elevating suspended solid loads during sporadic rain-driven events.

Productivity and food web structure of all ecosystems are strongly influenced by patterns of nutrient cycling and transport. Increased input of nutrients to the Everglades has resulted in adverse effects and a dramatic shift from diverse herbaceous communities to communities dominated by a few invasive exotic and native species (Davis 1994, David 1996, Porter and Porter 2002). Nutrient enrichment in estuarine systems has resulted in loss of seagrasses, algal blooms, and lethal low oxygen levels or anoxic events. Increases in areas of low dissolved oxygen and shifts in species composition of benthic invertebrates to more pollution-tolerant organisms are linked to increased nutrient levels (Barbour et al. 1996).

Contaminants include pesticides, fungicides, herbicides, microorganisms from sewage treatment plants, oils, greases, mercury, and other heavy metals such as copper and zinc. They can be introduced into the system from boating, as well as urban development and agricultural practices. Zooplankton and fish show direct toxic effects of these contaminants. Indirect effects can occur through the process of bioaccumulation or biomagnification through the food web, increasing toxic load to top predators (Day et al. 1989). Influx of contaminants and toxins is also altering water quality for human consumption.

Water clarity is affected by increased phytoplankton production, suspended solid loading, and sediment suspension. Phytoplankton production, which is stimulated by elevated nutrients, increases water color. Suspended solids that result from erosion and sediment suspension increase turbidity. Increased turbidity and water color can lead to SAV reduction.

Reduced Spatial Extent and Fragmentation. Drainage of wetlands and subsequent conversion of land into agricultural and urban uses have reduced total spatial extent of natural habitat and fragmented existing habitat within inland Everglades regions. Space was one physical characteristic that was necessary for all other physical and ecological components of these systems to be in place; it is the foundation of the mosaic of habitats in a low profile terrain (Craighead 1971, DeAngelis and White 1994). Loss of spatial extent has reduced the range of habitat options available for faunal populations (DeAngelis and White 1994). Extensive space was necessary for supporting robust numbers of higher vertebrates, such as wading birds and alligators, requiring large feeding and hunting ranges during different seasons and a range of hydrologic conditions in the nutrient-poor system (Browder 1976, Mazzotti and Brandt 1994). Fragmentation and habitat loss affects populations by reducing spatial extent of their prey base where it no longer supports viable populations. In many cases, due to development, lost spatial extent and connectivity of habitat cannot be restored on a large scale and must influence expectations for ecosystem restoration.

Physical Alterations. Construction of water-management canals and structures and resulting compartmentalization have affected both inland and estuarine regions. Compartmentalization by the system of canals and levees in inland regions has substantially disrupted natural patterns of sheet-flow direction, location, timing, and volume. Natural vegetation mosaic and habitat ranges of native animal species have been affected. Construction of canals has altered freshwater flow to estuaries and increased transport of nutrients, contaminants, and suspended solids. Water-control structures have decreased spatial extent of some estuaries and interfered with migration patterns of many estuarine species by acting as a barrier between the freshwater and saltwater habitats. Physical alterations have been made to the estuaries, including opening and widening of inlets, dredging and maintenance of navigation channels, development of shoreline and interior basins, and draining and filling of wetlands. Construction and dredging of canals stirs up sediments, reducing water clarity, and severely disrupts benthic communities.

Exotic Species. Introduction, both intended and unintended, of non-native species of plants and animals has resulted in a dramatic shift in plant community structure, loss of tree island habitat, and localized shifts in animal community structure, especially fish communities. Spread of these non-native species has been facilitated by stressors on the system.

Alterations in habitat, hydrology, and water quality have facilitated spread of exotic vegetation. Exotic species invade areas where dominant native vegetation has been damaged or stressed, allowing light penetration for exotic species germination. Lowered water tables result in transition from wetland to upland environments, and corresponding stress allows plants such as *Melaleuca* (*Melaleuca quinquenervia* (Cav.) Blake) to become established. Tree islands have been invaded with Brazilian pepper (*Schinus terebinthifolius* Raddi), *Melaleuca*, and Old World climbing fern (*Lygodium microphylla* (Cav.) R.Br.). Increased nutrient concentrations can produce dramatic shifts from diverse herbaceous communities to communities dominated by a few invasive exotic and nuisance native species, such as cattails (*Typha* spp.) and willows (*Salix* spp.). Introduction of nutrients also allows *Hydrilla* sp., water hyacinths (*Eichhornia crassipes* (Mart.) Solms) and water lettuce (*Pistia stratiotes* Linnaeus) to expand in open waters. *Melaleuca* and torpedograss (*Panicum repens* Linnaeus), have expanded over large areas of Lake Okeechobee, displacing native plants.

Animal communities most affected by exotic species invasion are fish communities (Trexler et al.

2001). Canals provide corridors of permanently flooded, deep-water habitat that would not otherwise occur and allow expansion of exotic and higher trophic level fishes into areas where they could not survive naturally (Howard et al. 1995). Introduction and spread of non-native fishes may alter dynamics of marsh fish communities, foraging behavior of wading birds, or genetic biodiversity. Prevalence of higher trophic fishes in canals may diminish the value of this habitat, which might serve as a dry season refugium for aquatic and amphibious fauna. Exotic fish and amphibian species prey on native species and compete with them for resources (Dineen 1984, Duever et al. 1986).

Boating and Fishing Pressure. As the population of South Florida has increased, so has recreational and commercial boating and fishing pressure. Boats traversing shallow flats and running aground result in seagrass scarring and sediment resuspension. Boat wakes erode banks of waterways, releasing solids into the waterway and damaging shoreline habitat. Dredging to increase navigation eliminates benthic organisms and SAV and increases suspended solids. Suspended solids created by wake erosion and dredging may cover productive adjacent bottom communities, suffocating residing organisms. Boat collisions are the leading cause of human-related manatee (*Trichechus manatus* Linnaeus) deaths (W. Dexter Render and Assoc. 1995). Fishing pressure from sport and commercial fisheries impacts standing stocks of many species (Post et al. 1999).

Attributes

The inland models and estuarine models require different attributes, but among the inland models and among the estuarine models, many similar attributes are used. Attributes that are used in most models, whether for an inland or an estuarine region, include wading birds and endangered and keystone species. Attributes common to only inland models include vegetation mosaic, periphyton mats, small aquatic fauna, and freshwater fish communities. Attributes common to only estuarine models include benthic communities, oysters, SAV, shoreline herbaceous wetlands, and mangrove habitats, fisheries, and nearshore reefs.

Wading Birds. Wading birds are good biological indicators throughout South Florida because of their close association with hydropattern. The current managed system has reduced nesting birds from 75 to 90 % compared to the 1930s. Numbers of snowy egrets (*Egretta Thula* Molina), tri-colored herons (*Egretta tricolor* Muller), white ibis (*Eudocimus albus* Linnaeus), and wood storks (*Mycteria Americana* Linnaeus) have relocated away from estuaries and into impounded central and northern Everglades. Also, white ibis and wood storks have altered the timing of nesting compared to historical patterns (Ogden 1994). It is hypothesized that the reduction in nesting birds correlates to a substantial decline in abundance and availability of aquatic prey base caused by water-management practices. For animals such as wading birds that operate over large spatial scales, compartmentalization and peripheral drainage have converted a single, expansive wetland system into several, smaller, hydrologically independent systems. Levees and canals have replaced shallowly flooded marsh edges with either overdrained or more deeply flooded marsh along levee slopes.

Endangered and Keystone Species. Many species are either unique to the South Florida ecosystem or are keystone animals at landscape and regional scales, and they are classified as attributes to the area, including the West Indian manatee, Florida panther (*Puma concolor coryi* Bangs), Everglades snail kite (*Rostrhamus sociabilis* Vieillot), Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis* Howell), American alligator, American crocodile, and pink shrimp (*Penaeus duorarum* Burkenroad). The manatee, panther, snail kite, seaside sparrow, and crocodile are listed on the endangered species list. Keystone species are those important to the overall health of the region. For example, alligators and crocodiles are often considered keystone species since their holes and trails provide important refugia for aquatic fauna during dry periods (Craighead 1968). They are top predators that greatly influence size, classes, distribution, and abundance of marsh animals.

Vegetation Mosaic. The vegetation mosaic in a given locale is primarily a function of climate, soil type, and suitable water conditions, including depth of water table, length and frequency of inundation, flow, and water quality. These plant communities, in turn, provide food and/or habitat for wildlife. Thus, changes in distribution, abundance, and species composition of plant communities have a direct effect upon type and quality of associated animal communities (Alexander and Crook 1975, McPherson et al. 1982, Sharitz and Gibbons 1989). Habitat loss directly impacts availability of resources required by organisms that use these areas. However, distribution of these habitats across the landscape is even more important because few organisms use only one habitat type, particularly in a seasonally fluctuating landscape. Models often target specific types of vegetation such as tree islands, marsh plant communities, and upland and wetland habitats as attributes.

Periphyton Mats. Periphyton is important as a food-web base, as habitat structure for fishes and invertebrates (Geddes and Trexler 2003), for oxygenating the water column, and in forming marl soils. Communities of green algae and diatoms may be especially important to periphyton grazers. Water-management practices and changes in water chemistry, including increased levels of total phosphorus, have changed spatial distribution and species composition of periphyton mats (Browder et al. 1994, Davis 1994). Shortened hydroperiods cause a reduction in proportion of diatoms and green algae and an increase in calcareous blue-green algae, thus reducing food value of periphyton and affecting productivity of the Everglades. In nutrient-enriched areas, species characteristic of low-nutrient waters are replaced by filamentous species.

Small Aquatic Fauna. Aquatic fauna of freshwater Everglades' marshes include myriad small fishes, amphibians, reptiles, crustaceans, snails, and other invertebrates that play enormously important roles in food webs, nutrient cycles, and energy transfers from primary consumers to the highest trophic levels in the ecosystem. Total abundance of aquatic fauna in the system has been greatly reduced due to combined effects of reduced spatial extent of wetlands, shortened hydroperiods, altered water recession rates, compartmentalization, and possible reductions in secondary production associated with shifts in periphyton composition (Dalrymple 1987, Browder et al. 1994, Davis et al. 1994, Loftus and Eklund 1994, Howard et al. 1995, Trexler and Jordan 1999, Turner et al. 1999, Trexler and Loftus 2000, Diffendorfer et al. 2001, Kobza et al. 2004, Trexler et al. 2005).

Freshwater Fish Communities. Population density of small marsh fishes in the Everglades is directly related to duration of uninterrupted flooding (Trexler and Loftus 2000), and maximum densities are reached only after multiple years of continual surface water (Loftus et al. 1990, Loftus and Eklund 1994, Turner et al. 1999). These small fishes are important links in the ecosystem, as they are a primary source of food for wading birds such as wood storks and roseate spoonbills (*Ajaia ajaja* Linnaeus) (Bjork and Powell 1994, Ogden 1994). Marsh fish are impacted by water flow, shortened hydroperiods, and reduced habitat.

Coastal Attributes

Benthic Communities. Benthic organisms provide essential ecological and biological functions in estuaries and can influence environmental quality. They are often used as water-quality indicators because they are primarily sedentary and, thus, have limited escape mechanisms to avoid disturbances (Bilyard 1987). They can provide an easily monitored record of effects of short- and long-term environmental changes through species composition and abundance changes. They have been used extensively as indicators of pollution and natural fluctuation impacts in estuarine environments (Gaston et al. 1985, Bilyard 1987, Holland et al. 1987, Boesch and Rabalais 1992).

Oysters. Oysters are an important component of benthic invertebrate communities and are treated as a separate attribute by most estuarine models. The Eastern oyster (*Crassostrea virginica* Gmelin) is the dominant species in oyster reef communities in South Florida. Oyster bars provide habitat and food for other species, including the oyster catcher (*Haematopus palliates* Temminck). Under natural conditions, oyster reefs can be very large and provide extensive attachment area for oyster spat and numerous associated species such as mussels, tunicates, bryozoans, and barnacles (Woodward-Clyde 1998). Over 40 species of macrofauna may be living in oyster beds (Bahr and Lanier 1981), with the total number of species exceeding 300 (Wells 1961). Oysters also create substrate to support other species and filter water to remove suspended materials. Individual oysters filter 4 to 34 liters of water per hour, removing phytoplankton, particulate organic carbon, sediments, pollutants, and microorganisms from the water column. This process results in greater light penetration, promoting growth of SAV immediately downstream from oyster bars.

Distribution and abundance of oysters are influenced by availability of planktonic food, water quality and clarity, salinity, and the presence of a suitable substrate for attachment of veliger larvae. They require salinity levels above 3–5 ppt, with an optimal salinity range between 12 and 28 ppt varying with geographical region (Loosanoff 1932, Chanley 1958, Galtsoff 1964, Woodward-Clyde 1998). Increased oligohaline conditions have limited distribution of oysters in South Florida estuaries. Also, higher salinity levels increase negative effects from saltwater predators such as oyster drills (*Stramonita* sp.) (Hofstetter 1977, White and Wilson 1996) and the protozoan parasite dermo (*Perkinsus marinus* Dermo), which is limited to salinities greater than 9 ppt and has been implicated as a cause of 50 percent of adult oyster mortality in Florida (Mackin 1962, Quick and Mackin 1971, Volety 1995). Thus, oyster distribution, health, and abundance reflect water quality, salinity, and substrate quality of an estuary (Andrews et al. 1959, Sellers and Stanley 1984, Lenihan 1999, Livingston et al. 2000).

Submerged Aquatic Vegetation. SAV is a critical food source for many species and foraging and hiding ground for others. It provides habitat for myriad animals, including juveniles of many commercially and recreationally valuable species (Zieman 1982). Seagrasses affect water quality through nutrient uptake and storage, binding of sediments by their roots, and trapping of particles within their leaf canopy. With growth of lush seagrass beds, these mechanisms drive the area towards a condition of clear water, lowering nutrients for algae growth and concentrations of suspended sediment in the water column. SAV requires sunlight to photosynthesize, thus murky water caused by silt, turbidity, color, or phytoplankton is stressful. SAV is intolerant of changes in salinity, toxicity, and water clarity and can be used to document changes within the ecosystem.

Shoreline Herbaceous Wetlands and Mangrove Habitats. Mangrove communities provide habitat for marine organisms, protect shorelines from erosion, and enhance water quality (Savage 1972). Detritus produced by mangroves is the basis of the food chain for South Florida's marine and estuarine ecosystems. Mangroves provide nursery grounds for sport and commercial fisheries, including spotted seatrout (*Cynoscion nebulosus* Cuvier), common snook (*Centropomus undecimulis* Bloch), and pink shrimp (Lindall 1973, Harris et al. 1983). Mangrove roots act to trap sediments and prevent shoreline erosion and provide attachment surfaces for various marine organisms. Additionally, mangrove forests provide habitat for a highly diverse population of birds (Odum et al. 1982). Also, these coastal wetlands help maintain water and habitat quality by filtering sediments and nutrients from inflowing waters.

Shoreline herbaceous wetlands and mangrove habitats have lost much of their spatial extent, connectivity, and ecological function through dredge-and-fill and drainage activities (Estevez 1998, National Safety Council 1998). In some areas, drainage for agricultural and urban development has reduced overland flows of fresh water to mangroves, and channelization has diverted fresh water away from coastal feeder streams and creeks, resulting in greater concentrated runoff that changes salinity balance, reduces flushing of detritus, and washing of nutrients directly into the estuary without the benefit of mangrove filtration (Estevez 1998).

Fisheries. Diversity and dimensions of stable fisheries are good indicators of the state of an ecosystem. At least 70 percent of Florida's recreationally and commercially sought fishes depend on estuaries for part of their life histories (Lindall 1973, Harris et al. 1983, Estevez 1998). Within the estuary, seagrass communities, mangroves, oyster reefs, and stable benthic communities provide critical refugia and food sources for juvenile fish such as redfish (*Sciaenops ocellatus* Linnaeus), grouper, snook and spotted seatrout. Decline in juvenile abundance and distribution of these and other species, along with overall decline in species richness may be related to fishing pressure and a decrease in suitable habitat and/or a result of alterations in salinity regime and timing of freshwater discharges (Christensen 1965, Browder and Moore 1981, M. Hedgepeth, South Florida Water Management District, pers. comm.).

Nearshore Reefs. Nearshore reefs form bands of unique marine habitat offshore of the Atlantic Coast and are included as attributes in eastern northern estuarine models. Reef development is typically slow and occurs over geologic time scales, so impacts to reefs may cause ecological problems that require long time frames for recovery. Nearshore reefs are adversely affected by high level discharges, resulting silt and salinity plumes, and possibly changes due to nutrient enrichment. Reefs provide habitat for many marine species of socio-economic value to tourism and local fisheries. Continental shelf fish biodiversity is influenced by various reef structures and is also susceptible to sedimentation.

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Manuscript received 7 March 2005; revisions received 7 July 2005; accepted 7 September 2005.

WETLANDS, Vol. 25, No. 4, December 2005, pp. 870–883

A CONCEPTUAL ECOLOGICAL MODEL OF FLORIDA BAY

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Abstract: Florida Bay is a large and shallow estuary that is linked to the Everglades watershed and is a target of the Greater Everglades ecosystem restoration effort. The conceptual ecological model presented here is a qualitative and minimal depiction of those ecosystem components and linkages that are considered essential for understanding historic changes in the bay ecosystem, the role of human activities as drivers of these changes, and how restoration efforts are likely to affect the ecosystem in the future. The conceptual model serves as a guide for monitoring and research within an adaptive management framework. Historic changes in Florida Bay that are of primary concern are the occurrence of seagrass mass mortality and subsequent phytoplankton blooms in the 1980s and 1990s. These changes are hypothesized to have been caused by long-term changes in the salinity regime of the bay that were driven by water management. However, historic ecological changes also may have been influenced by other human activities, including occlusion of passes between the Florida Keys and increased nutrient loading. The key to Florida Bay restoration is hypothesized to be seagrass community restoration. This community is the central ecosystem element, providing habitat for upper trophic level species and strongly influencing productivity patterns, sediment resuspension, light penetration, nutrient availability, and phytoplankton dynamics. An expectation of Everglades restoration is that changing patterns of freshwater flow toward more natural patterns will drive Florida Bay's structure and function toward its pre-drainage condition. However, considerable uncertainty exists regarding the indirect effects of changing freshwater flow, particularly with regard to the potential for changing the export of dissolved organic matter from the Everglades and the fate and effects of this nutrient source. Adaptive management of Florida Bay, as an integral part of Everglades restoration, requires an integrated program of monitoring, research to decrease uncertainties, and development of quantitative models (especially hydrodynamic and water quality) to synthesize data, develop and test hypotheses, and improve predictive capabilities. Understanding and quantitatively predicting changes in the nature of watershed-estuarine linkages is the highest priority scientific need for Florida Bay restoration.

Key Words: ecosystem restoration, estuaries, Florida Bay, Everglades, adaptive management, seagrass, freshwater flow, salinity effects

BACKGROUND

Florida Bay is a triangularly shaped estuary, with an area of about 2200 km^2 that lies between the southern tip of the Florida mainland and the Florida Keys (Figure 1). About 80% of this estuary is within the boundaries of Everglades National Park and much of the remainder is within the Florida Keys National Marine Sanctuary. A defining feature of the bay is its shallow depth, which averages about 1 m (Schomer and Drew 1982). Light sufficient to support photosynthesis can reach the sediment surface in almost all areas of the bay, resulting in dominance of seagrass beds as both a habitat and a source of primary production. The shallowness of Florida Bay also affects its circulation and salinity regime. Except for basins near the northern coast (near freshwater sources), the bay's water column is vertically well-mixed and usually isohaline. In contrast, its complex network of shallow mud banks restricts horizontal water exchange among the bay's basins and between these basins and the Gulf of Mexico (Smith 1994, Wang et al. 1994). In areas with long residence times, the salinity of Florida Bay water can rise rapidly during drought periods due to excess of evaporation over precipitation and freshwater inflow (Nuttle et al. 2000). Salinity levels as high as twice that of seawater have been measured (McIvor et al. 1994). Another defining feature of the bay is that its sediments are primarily composed of carbonate mud, which can scavenge inorganic phosphorus from bay waters (DeKanel and Morse 1978).

Until the 1980s, Florida Bay was perceived by the public and environmental managers as being a healthy and stable system, with clear water, lush seagrass beds, and highly productive fish and shrimp populations. In the mid-1980s, however, catches of pink shrimp decreased dramatically (Browder et al. 1999), and in 1987, a mass mortality of turtle grass (*Thalassia testudinum* Banks & Soland ex. Koenig) beds began (Robblee et al. 1991). By 1992, the ecosystem appeared to change from a clear water system, dominated by benthic primary production, to a turbid water system, with algae blooms and resuspended sediments in the water column. The conceptual ecological model presented here focuses on these changes in seagrass communities and water quality as central issues to be considered by environmental managers.

The Florida Bay Conceptual Ecological Model is one of eleven regional models that are being used as tools for synthesis, planning, assessment, and communication within the adaptive management framework of the Everglades Restoration Plan. This framework and a summary of all of the conceptual ecological models are described in Ogden et al. (2005). Overviews of the history and challenges of Everglades restoration are presented in Ogden et al. (2005) and Sklar et al. (2005). The format and symbols of the Florida Bay model follows that of Ogden et al. (2005) and the other conceptual models published in this issue of *Wetlands*. Furthermore, the organization of this paper follows the conceptual model diagram, with major sections on drivers and stressors, and ecological attributes (generally structural components of the ecosystem) and their links to stressors. A final section considers expectations and uncertainties regarding future responses to restoration efforts.

This simple model does not address spatial complexity in Florida Bay. Florida Bay is, indeed, not so much a singular estuary, but a complex array of more than forty basins, with distinct characteristics, that are partitioned by a network of mud banks and islands (Schomer and Drew 1982, Fourqurean and Robblee 1999). The structure of vegetative habitats, as well as water quality and ecosystem processes, vary distinctly with this spatial variation. Nevertheless, only a single, generic model is described and intended to summarize the main characteristics and trends of the bay. While the structure of this model is appropriate for most areas of the bay, the relative importance of model components differ considerably among subregions. Any application of this model (e.g., recommendations for a specific set of monitoring parameters and guidelines) must accommodate the degree of spatial variability of the bay.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

Following observations of Florida Bay's dramatic ecological changes in the 1980s, it was commonly assumed that a direct cause of these changes was a long-term increase in salinity, which in turn was caused by the diversion of freshwater away from Florida Bay via South Florida Water Management District canals. However, subsequent research has indicated that these ecological changes may not be attributable to a single cause. While decreased freshwater inflow and resultant increased salinity have been part of the problem, it appears that other human activities, as well as natural forces, may have also played a role (Boesch et al. 1993, Armentano et al. 1997, Fourqurean and Robblee 1999). The conceptual ecological model presented here includes both natural and anthropogenic sources of stress (Figure 2). The discussion of external drivers and ecological stressors below is organized by stressor (ovals in Figure 2), with consideration of the main drivers (rectangles in Figure 2) that influence each stressor.

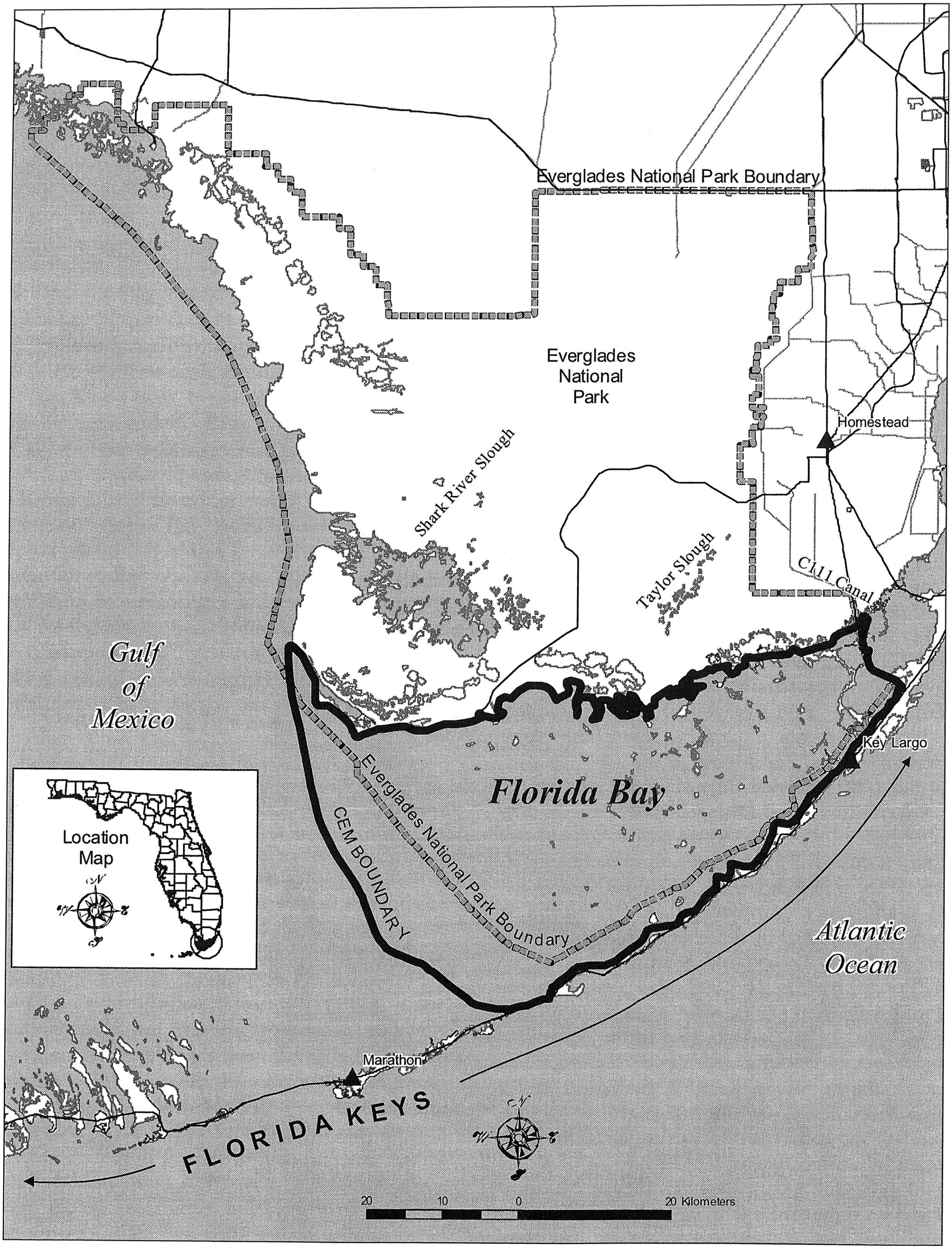

Figure 1. Geographic setting and boundary of the Florida Bay Conceptual Ecological Model (CEM).

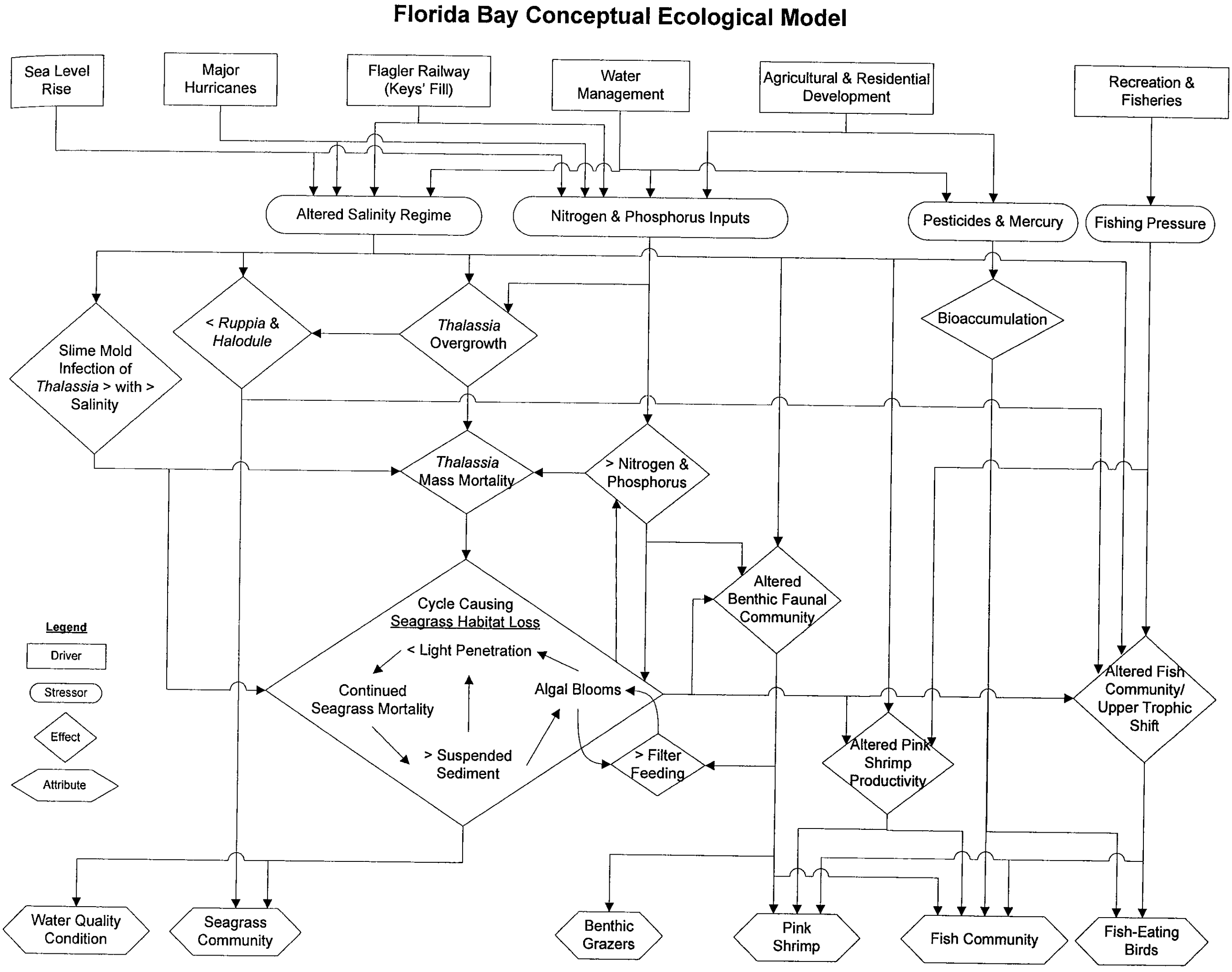

Figure 2. Florida Bay Conceptual Ecological Model Diagram. The format of this figure follows Ogden et al. (2005). Rectangles represent major external drivers of ecological change, ovals represent ecological stressors, diamonds represent ecological linkages and functions that mediate the effect of stressors on attributes, and hexagons represent ecosystem attributes to be monitored as part of the adaptive assessment process. Increases or decreases noted in diamonds with "< *Ruppia* and *Halodule*" and "> Nitrogen and Phosphorus" refer to pre-restoration changes.

Altered Salinity Regime

Florida Bay's salinity regime varies greatly over time and space. This variation ranges from coastal areas that can be nearly fresh during the wet season, to large areas of the central bay that can have salinity levels near 70 psu during prolonged droughts, to nearly stable marine conditions (about 35 psu) on the western boundary of the bay or near Florida Keys' passes. The main factors that determine the salinity regime in the bay are the inflow of freshwater from the Everglades, the difference between rainfall and evaporation over the bay, and exchange with marine waters of the Gulf of Mexico and Atlantic Ocean. Both freshwater inflow and exchange with the Atlantic have changed drastically in the past hundred years, resulting in an alteration of the bay's salinity regime (Swart et al. 1999, Brewster-Wingard et al. 2001, Dwyer and Cronin 2001).

Freshwater inflow to Florida Bay decreased in volume and changed in timing and distribution during the twentieth century because of water management. Hydrologic alteration began in the late 1800s but accelerated with construction of drainage canals by 1920, the Tamiami Trail by 1930, and the Central and South Florida (C&SF) Project and the South Dade Conveyance System from the early 1950s through 1980 (Light and Dineen 1994). With diversion of freshwater to the Atlantic and Gulf of Mexico coasts to the north, the bay's mean salinity inevitably increased. Isotopic studies of carbonate preserved in coral skeletons and buried ostracod shells confirmed this trend (Swart et al. 1999, Dwyer and Cronin 2001). Paleoecological studies also indicated that salinity variability within the bay also changed during the twentieth century, with an increase in variability in the northeastern bay, where freshwater inflows are channelized (Brewster-Wingard et al. 2001), and a decrease in variability in the southern bay (Swart et al. 1999).

Paleoecological studies indicated that a cause of salinity changes in the southern bay was construction of the Flagler Railway across the Florida Keys from 1905 to 1912 (Swart et al. 1996, 1999). In the nineteenth century, prior to railway construction and water management, southern Florida Bay had a lower mean salinity and more frequent periods of low (10 psu–20 psu) salinity than during the twentieth century. The extent and frequency of high salinity events in the southern bay does not appear to have changed between centuries. The bay's salinity regime changed abruptly around 1910 because passes between the Keys were filled to support the railway. Thus, water exchange between Florida Bay and the Atlantic Ocean was decreased, and this probably caused an increase in water residence time and a change in water circulation patterns within the bay.

Two important natural controls of salinity, sea-level rise and the frequency of major hurricanes, must also be considered. Florida Bay is a very young estuary, the product of sea level rising over the shallow slope of the Everglades during the past 4,000 years (Wanless et al. 1994). With rising sea level, the bay not only became larger but also became deeper. With greater depth, exchange of water between the ocean and the bay increased. All else being equal, this would result in a more stable salinity regime with salinity levels increasingly similar to the ocean. However, a factor that has counteracted rising sea level is accumulation of sediment, which makes the bay shallower. Most sediment that accumulates in Florida Bay is carbonate precipitated from water by organisms living in the bay (Bosence 1989). The extent to which these sediments accumulate is a function of the biology of these organisms (including skeletal carbonate production), chemical dynamics in the water column and sediments, and the physical energy available to transport some of these sediments from the bay. Major hurricanes are thought to be important high-energy events that can flush the bay of accumulated sediments. However, since 1965, no major hurricane has directly affected Florida Bay. Resultant sediment accumulation, with associated alteration of depth, circulation patterns, residence time, salinity, and nutrient storage may have influenced ecological changes in recent decades.

Nitrogen and Phosphorus Inputs

Productivity and food-web structure in all ecosystems are strongly influenced by internal nutrient cycling and import and export of these nutrients. Throughout the world, estuarine ecosystems have undergone dramatic ecological changes because they have been markedly enriched by nutrients derived from human activity (National Research Council 2000). These changes have often been catastrophic, with loss of seagrasses, increased algal blooms, and increased incidence of hypoxic and anoxic events. Augmentation of nitrogen and phosphorus inputs to an estuary is a potentially important stressor.

The degree to which nitrogen and phosphorus inputs have stressed Florida Bay is unclear. In general, the bay is relatively rich in nitrogen and poor in phosphorus, especially towards the eastern region of the bay (Boyer et al. 1997). This spatial pattern is at least partly a function of natural biogeochemical processes (e.g., P retention by the bay's carbonate sediments and relatively low N in adjacent marine waters) and thus may have existed prior to recent human influences. Little direct evidence confirms that nutrient inputs to the bay or concentrations within the bay have increased during the past century, but with expanding agricultural and residential development in South Florida, and particularly development of the Florida Keys, some nutrient enrichment almost certainly has occurred (Lapointe and Clark 1992, Orem et al. 1999). Anthropogenic nutrients that enter Florida Bay are derived not only from local sources (fertilizers and other wastes from agricultural and residential areas), but also from remote sources. Contributions of nutrients from atmospheric deposition and from the Gulf of Mexico, which may include nutrients from the phosphate fertilizer industry of the Tampa-Port Charlotte area and residential development from Tampa to Naples, are significant external nutrient sources (Rudnick et al. 1999).

Different sub-regions of the bay are differentially influenced by these local or remote sources, depending on the magnitude of inputs, relative abundance of different nutrients, internal cycling pathways and rates, and water residence time (Boyer et al. 1997, Rudnick et al. 1999, Childers et al. 2005). Algal bloom occurrence in the central and western bay is influenced by a combination of these factors (Tomas et al. 1999, Brand 2002). Despite the lack of definitive data, it is, nevertheless, a reasonable hypothesis that a chronic increase in nutrient inputs occurred in Florida Bay in the twentieth century and that this increase contributed to the bay's recent ecological changes. Development of a water quality model driven by appropriately scaled hydrodynamic and hydrologic models is essential to understand and evaluate quantitatively the potential effects of past nutrient inputs and predict the effects of future management scenarios.

Water management is a driver of nutrient stress in that the canal system can transport materials through wetlands toward the bay, decreasing nutrient retention by wetlands and thereby increasing inputs to the bay. Altered nutrient transport via canals may also alter the chemical composition of nutrients entering the bay. These inputs from the Everglades and the Gulf of Mexico are affected not only by changes of freshwater flowing from Taylor Slough and Shark River Slough, but also by changes in the bay's circulation. Nutrient cycling and retention within the bay are sensitive in particular to changes in residence time (a function of circulation) that were caused by Flagler Railway construction, as well as the balance of sea-level rise and sedimentation or sediment removal by major hurricanes. Hurricanes may be particularly important, as nutrients (organic and inorganic) can accumulate in sediments, and the absence of major hurricanes during the past few decades may have resulted in an accumulation of nutrients.

Pesticides and Mercury

With the widespread agricultural and residential development of South Florida, application and release of pesticides and other toxic materials has increased. Deposition of mercury from local and global sources has also increased in the past century and is of particular concern because of high concentrations of methylmercury in upper trophic level species (Cleckner et al. 1998). Altered biogeochemistry resulting from changes in water quality (e.g., sulfate availability), which in turn affects methylation rates, has also played a role in increased mercury bioaccumulation (Cleckner et al. 1999). Pesticides and mercury are of concern because they can affect human health through consumption of fish or other biota with high concentrations of these toxins and because other species also may be adversely affected by these compounds. To date, no evidence links observed ecological changes in Florida Bay to inputs of toxic compounds. Nevertheless, endocrine-disrupting endosulfans, with concentrations that could have biological effects, have been found in upstream canals and the biota of associated lakes (Scott et al. 2002, G. Graves, personal communication). Additionally, mercury levels remain elevated in fish in eastern Florida Bay despite decreases observed elsewhere (Strom and Graves 2001, Evans et al. 2003). Water management affects the distribution of these toxic materials and potentially their transport to Florida Bay (Scott et al. 2002, Rumbold et al. 2003). Controlling water levels in wetlands may also influence the decomposition of pesticides and mercury methylation rates because these processes are sensitive to the presence of oxygen and sulfate in soils, which are affected by water levels.

Fishing Pressure

For any species that is the target of recreational or commercial fishing, fishing pressure directly affects population dynamics and community structure. Commercial fishing has been prohibited within Everglades National Park since 1985, but populations that live outside of the Park boundaries for at least part of their life cycle, including most of Florida Bay's sportfish species, are affected by fisheries (Tilmant 1989). Recreational fishing pressure within the Park also affects these populations (e.g., the size structure of the gray snapper assemblages [Faunce et al. 2002]).

ECOLOGICAL ATTRIBUTES

The set of Florida Bay's attributes presented here (hexagons in Figure 2) includes both indicators of ecosystem condition and attributes deemed to be intrinsically important to society. Attributes, in most cases, are biological components of the ecosystem, including seagrass, mollusks, shrimp, fish, and birds, but also an aggregated attribute (water-quality condition) that includes phytoplankton blooms, turbidity, and nutrient concentrations. While the list of biological components is broad, it is clear from their links to stressors (see diamonds and associated arrows, linking to stressors in ovals, in Figure 2) that these attributes are not equally weighted; the most significant and causally interconnected attribute of this conceptual ecological model is the seagrass community. Details of each attribute and its linkages to the conceptual model's set of stressors are given below.

Seagrass Community

The structural and functional foundation of the Florida Bay ecosystem is its seagrass community (Zieman et al. 1989, Fourqurean and Robblee 1999). These plants are not only a highly productive base of the food web, but are also a principal habitat for higher trophic levels and strongly influence the physical and chemical nature of the bay. Understanding how seagrasses affect water quality is essential to understanding the bay's current status and predicting its response to restoration and other human activities.

Seagrasses affect water quality by three mechanisms: nutrient uptake and storage, binding of sediments by their roots, and trapping of particles within their leaf canopy. With growth of dense seagrass beds, these mechanisms drive the bay towards a condition of clear water, with low nutrient availability for algae growth within the water column and low concentrations of suspended sediment in the water. Paleoecological studies and historic observations suggest that *T. testudinum* in Florida Bay proliferated and increased in density during the mid-twentieth century (Brewster-Wingard and Ishman 1999, Zieman et al. 1999, Cronin et al. 2001), while other common species (*Halodule wrightii* Aschers and *Ruppia maritima* Linnaeus) likely decreased in distribution and density. From the 1960s through the mid-1980s, dense *T. testudinum* beds expanded throughout central and western Florida Bay, and the water column was reported to be crystal clear (Zieman et al. 1999). Largely following the conceptual model of Zieman et al. (1999), we hypothesize that with the onset of a *T. testudinum* mass-mortality event in 1987 (Robblee et al. 1991), the three mechanisms given above reversed, initiating a cycle (large diamond in Figure 2) that contributed to additional seagrass habitat loss (or at least inhibited recolonization) and favored the persistence of more turbid water with episodic algal blooms (Stumpf et al. 1999).

Causes of the 1987 mass-mortality event can be considered at two time scales—a multi-decadal period that poised *T. testudinum* beds for collapse and a short-term period (of days–months) in 1987 when proximate factors triggered mortality (Zieman et al. 1999). We hypothesize that changes in two stressors, salinity and a chronic and low-level increase in nutrient availability, occurred over several decades and caused *T. testudinum* beds to grow to an unsustainable density (designated "overgrowth" in Figure 2) by the mid-1980s. It is also likely that a decrease in shoal grass (*Halodule wrightii*) and widgeon grass (*Ruppia maritima*) occurred with the *T. testudinum* increase. *Thalassia testudinum* overgrowth may have occurred because the species had a competitive advantage over other seagrass species when the bay's salinity regime was stabilized, with few periods of low salinity (Zieman et al. 1999). Nutrient enrichment also may have played a role, with a chronic accumulation of nutrients caused by increased inputs over decades or decreased outputs because of the absence of major hurricanes or closure of Florida Keys' passes. Once *T. testudinum* beds were poised for collapse, multiple factors that acted over a short time scale are hypothesized to have been a proximate cause of mortality in 1987. These factors are thought to be related to high respiratory demands of dense grass beds and accumulated organic matter. During the summer of 1987, with high temperatures and hypersaline water, respiratory demand may have exceeded photosynthetic production of dissolved oxygen, causing sulfide concentrations to increase to lethal concentrations (diagram from Durako et al. in McIvor et al. 1994, Carlson et al. 1994). This hypothesis regarding the proximate cause of seagrass mass mortality is supported by a recent *in situ* study in Florida Bay (Borum et al. 2005) that showed the importance of anoxia and sulfide in surficial sediments as a potential cause of *T. testudinum* mortality.

Regardless of the cause of the mass-mortality event, once this event was initiated, the ecology of Florida Bay changed. A cycle resulting in continuing seagrass habitat loss is depicted in the conceptual ecological model. Continued seagrass mortality results in increased sediment resuspension (Prager and Halley 1999, Stumpf et al. 1999) and increased nutrient (nitrogen and phosphorus) release from sediments, stimulating phytoplankton growth in the water column. The presence of both phytoplankton and suspended sediment result in decreased light penetration to seagrass beds. This decreased light can limit seagrass growth and sustain the feedback loop.

Dynamics of this feedback loop are probably not independent of the salinity regime. Seagrass wasting disease, caused by a slime mold (*Labyrinthula* sp.) infection, is more common at salinities near or greater than seawater ($\geq$ 35 psu) than at low (15 to 20 psu) salinities (Blakesley et al. 2003). High salinity may have played a role in the initial seagrass mass mortality event but more likely has served to promote seagrass re-infection since that event. Incidence of this disease may therefore be directly affected by water management actions.

If the state of the seagrass community is to be used as a criterion to decide success of environmental restoration efforts, scientists and managers must specify the desirability of alternative states. Based on studies of historic changes of seagrass communities in Florida Bay and anecdotal information (Brewster-Wingard and Ishman 1999, Zieman et al. 1999, Cronin et al. 2001), it is likely that the Florida Bay of the 1970s and early 1980s, with lush *T. testudinum* and clear water, was probably a temporary and atypical condition. From an ecological perspective, restoration should generally strive for a more diverse seagrass community with lower *T. testudinum* density and biomass than during that anomalous period. A diversity of seagrass habitat is expected to be beneficial to many upper trophic level species (Thayer et al. 1999).

Water Quality Condition

Water quality condition reflects the light field, nutrient availability in the ecosystem, and algal blooms in the water column. All of these characteristics are closely related to the condition of seagrasses and food web structure and dynamics of the bay. While these characteristics have been monitored and researched since the early 1990s, earlier information is scarce for salinity and almost non-existent for the above water quality characteristics. Thus, at the present time, we do not know whether nutrient inputs to the bay have actually increased in recent decades or whether periods with sustained algal blooms and high turbidity occurred in the past.

Studies of nutrient export from southern Everglades canals and creeks flowing into Florida Bay have provided insights regarding the relationship between patterns of freshwater discharge, nutrient dynamics, and output to Florida Bay (Rudnick et al. 1999, Davis et al. 2003, Sutula et al. 2003). Results show that phosphorus loads to the bay do not greatly increase with increased freshwater inputs to the bay, but given the phosphorus limitation of the eastern bay, any increase in phosphorus availability is likely to affect productivity patterns. Unlike phosphorus, total nitrogen loads probably do increase with more freshwater flow (Rudnick et al. 1999), and algal growth in western and sometimes central Florida Bay can be nitrogen limited (Tomas et al. 1999). The potential thus exists for hydrologic restoration to increase nitrogen loading and stimulate phytoplankton blooms (Brand 2002). Because most of the nitrogen that is exported from the Everglades to the bay is in the form of organic compounds (Rudnick et al. 1999), the fate of these compounds within the bay is a critical unknown; if these compounds are easily decomposed and their nitrogen becomes available to algae, then increased freshwater flow could stimulate algal growth. In addition to organic nitrogen decomposition rates, other critical unknowns regarding the availability of nitrogen for algal productivity include rates of nitrogen fixation and denitrification within the bay and the residence time of water in bay's sub-basins.

Finally, as emphasized earlier, light penetration through Florida Bay waters is a key to the health of seagrasses. Light penetration is largely a function of turbidity from algae and suspended sediment. Although light levels were potentially limiting to seagrass growth during the early and mid-1990s, in more recent years, only the northwest corner of the bay is potentially light-limiting (Kelble et al. 2005). For successful restoration of Florida Bay, light penetration must be sufficient to ensure viable seagrass habitat. Such a light-penetration criterion has been used in other estuaries (Dennison et al. 1993) and is an important success criterion for Florida Bay.

Benthic Grazers

Consumption of phytoplankton by bivalves and other benthic filter feeders and suspension feeders (especially sponges and tunicates) may have significant impacts on the distribution, magnitude, and duration of algal blooms. Increases or decreases in algal blooms may be related to significant increases or decreases in grazer abundance and biomass. Decreased grazing may have occurred in the 1990s because of seagrass habitat loss, which could have decreased grazer abundance. Additionally, grazers may have been negatively affected by cyanobacterial blooms (*Synechococcus* sp., the dominant phytoplankter in central Florida Bay's blooms [Phlips and Badylak 1996]). These blooms may have played a role in the large-scale mortality of sponges in southern Florida Bay in the early 1990s (Butler et al. 1995). Such a loss of grazers would have enabled larger blooms to occur, decreasing light penetration, and thereby reinforcing the feedback loop of seagrass mortality and algal blooms.

Benthic grazers abundance, biomass, species composition, and distribution are valuable in a monitoring program not only because of their functional link with phytoplankton blooms, but also because these grazers are ecological indicators. Paleoecological and recent studies of the bay have inferred that long-term changes in molluscan species composition are largely a function of salinity and seagrass habitat availability (Brewster-Wingard and Ishman 1999).

Pink Shrimp

Pink shrimp (*Farfantepenaeus duorarum* Burkenroad) are economically important to society as a highly valued fishery species and are also ecologically important as a major dietary component of game fish and wading birds. Furthermore, pink shrimp are an indicator of Florida Bay's productivity because the bay and nearby coastal areas are primary shrimp nursery grounds. This nursery supports the shrimp fishery of the Tortugas grounds (Ehrhardt and Legault 1999). Hydrologic and ecological changes in the Everglades and Florida Bay may have impacted this fishery, which experienced a decrease in annual harvest from about 4.5 million kg per year in the 1960s and 1970s to only about 0.9 million kg per year in the late 1980s (Ehrhardt and Legault 1999). This decrease may have been associated with seagrass habitat loss or high salinity (50 to 70 psu) during the 1989–1990 drought; experiments have shown that pink shrimp mortality rates increase with salinities above about 35 psu, and growth rates are optimal at 30 psu (Browder et al. 2002). Shrimp harvest statistics indicate that shrimp productivity increases with increasing freshwater flow from the Everglades (Browder 1985). This may be because greater freshwater inflows reduce the frequency, duration, and spatial coverage of hypersaline events in Florida Bay (Browder et al. 1999, 2002). The statistical relationship between indices of freshwater flow and shrimp productivity is sufficiently robust to be used by the National Marine Fisheries Service in management of the offshore fishery (Sheridan 1996).

Fish Community

The health of Florida Bay's fish populations is of great importance to the public; sport fishing is a major economic contributor to the region (Tilmant 1989). Recruitment, growth, and survivorship of these fish populations are affected by many factors, including salinity, habitat quality and availability, food-web dynamics, and fishing pressure. Changes in mangrove and seagrass habitats are likely to influence the structure and function of the fish community. However, seagrass mass mortality appears to have had a greater influence on fish community structure than on the absolute abundance of fish; no dramatic bay-wide decreases in fish abundance were observed along with seagrass mass mortality (Thayer et al. 1999). Rather, a shift in fish species composition occurred as a result of seagrass habitat loss and sustained algal blooms. When demersal fish markedly declined, pelagic fish such as the bay anchovy, which feed on phytoplankton, increased (Thayer et al. 1999). More recently, changes in the opposite direction have been observed (Powell et al. 2001). While causes of these changes are not well-established, there is no question that stressors, such as altered salinity regimes, not only affect upper trophic level populations directly but also affect them indirectly through habitat and food-web changes.

Another important stressor that needs to be considered with regard to fish populations is the impact of pesticides and mercury. As concentrations of mercury and some pesticides greatly increase in upper trophic level species, such as sport fish (via the process of bioaccumulation) that people eat, a human health issue potentially exists. Pesticides and mercury can also have ecological impacts by physiologically stressing organisms (particularly reproductive functions). While toxic contaminant inputs to Florida Bay do not appear to be associated with recent large-scale changes in the bay ecosystem, biotic exposure to toxicants could change in association with restoration-related changes in upstream water management.

Among the many fish species that could be used as indicators of the health of the ecosystem's upper trophic level, the spotted sea trout (*Cynoscion nebulosus* Cuvier in Cuvier and Valenciennes) is unique because it is the only major sport fish species that spends its entire life in the bay (Rutherford et al. 1989). Changes in the bay's sea trout population and toxic residues in this species thus reflect changes in the bay itself, as well as upstream restoration actions that affect the quantity and quality of water entering the bay. Sea trout are a particularly good restoration indicator for central Florida Bay, where they are commonly found and where prolonged periods of hypersalinity are common. This species is known to be sensitive to hypersalinity; density of post-larvae has been found to be greatest at an intermediate salinity range of 20–40 psu (Alsuth and Gilmore 1994). For northeastern Florida Bay, the abundance of common snook (*Centropomus undecimalis* Bloch), red drum (*Sciaenops ocellatus* Linnaeus, 1766), crevalle jack (*Caranx hippos* Linnaeus), and mullet are also being considered as potential restoration indicators.

Fish-Eating Birds

Florida Bay and its mangrove coastline are important feeding and breeding grounds for waterfowl and wading birds. Conceptual ecological models for other regions of the Everglades, particularly the Everglades Mangrove Estuaries Conceptual Ecological Model (Davis et al. 2005), present more detailed descriptions of the use of bird populations as ecological indicators and consider a wide variety of birds. For the Florida Bay Conceptual Ecological Model, we consider only fish-eating birds that are characteristic of the marine environment, such as great white herons, reddish egrets, osprey, brown pelicans, and cormorants. These birds are important predators within the bay and are potentially impacted by any stressors that affect their prey base, including salinity changes, nutrient inputs, toxic compounds, and fishing pressure. As with other top predators, these bird species may also be especially vulnerable to toxic contaminants.

RESTORATION RESPONSES: EXPECTATIONS AND UNCERTAINTIES

In this section, we present a prospective view of Everglades restoration. The Conceptual Ecological Model, while largely based on past ecological dynamics, still serves as a guide. The foremost purpose of this section is to identify those components and linkages (with associated ecological processes) that are most sensitive to changing watershed management, have a strong effect on the entire estuarine ecosystem, and yet are poorly understood relative to the information needs of the adaptive management process. This includes consideration of salinity and hydrodynamics, nutrient inputs and phytoplankton blooms, and benthic habitat and higher trophic level responses to restoration. Working hypotheses regarding each of these high priority aspects of the Florida Bay conceptual model are also presented here. We use the term ''working hypothesis'' in the sense that the described predictions and relationships, while generally not test-able with strict experimental control, can be assessed as part of a long-term adaptive management program.

Salinity Responses

The conceptual model explicitly illustrates the central importance of water management on the Florida Bay ecosystem, largely mediated through changing salinity. An expectation of the Everglades restoration plan is that salinity in the bay will decrease, expanding the spatial extent and duration of oligohaline to polyhaline conditions, while decreasing the extent and duration of hypersaline conditions. However, a quantitative understanding of the relationship between wetland hydrologic conditions, freshwater flow, and resultant salinity throughout the bay is still lacking. An important step toward gaining this understanding and a predictive capability for environmental management is the synthesis of a broad array of available hydrologic, hydrodynamic, and salinity information within a hydrodynamic model. Development of such a model is challenging, given the shallow and complex morphology of Florida Bay. To date, restoration planning has only used simple statistical estimates of salinity, largely as a function of wetland water stages, and these estimates have been limited to near-shore embayments. Predicting salinity change within the entire bay requires understanding of changing water inputs, exchanges, and circulation. The effects of restoration efforts thus will be strongly influenced not only by changing freshwater flow, but also by sea-level rise and changing bay morphology.

Working Hypotheses: Relationships of Mud Bank Dynamics, Sea-Level Rise, and Circulation. Circulation and salinity patterns, and thus ecological patterns, are strongly influenced by Florida Bay's mud banks, which are dynamic features. The response of these banks to sea-level rise and the changing frequency and intensity of tropical storms cannot confidently be predicted. Based on the persistence of mud-bank spatial distributions over centuries and past patterns of accretion (Wanless and Tagett 1989), we hypothesize that sediments will accrete on banks at rates comparable to rates of sea-level rise and that the spatial pattern of banks and basins will remain largely unchanged in future decades, despite the likelihood that tropical storm activity will increase during the coming decade (Goldenberg et al. 2001). If these hypotheses are true, then water circulation within the bay will continue to be restricted by mud banks, even with sea-level rise, and exchange of bay water with seawater of the Atlantic Ocean and Gulf of Mexico will not markedly increase. However, as the depth of basins increases (historic sediment accretion of banks has greatly exceeded sediment accretion in basins; Wanless and Tagett (1989)), the residence time of water in basins and the potential for stratification and oxygen stress would also increase. Moreover, with increased depth, light penetration to seagrass communities would decrease. Alternatively, if mud bank accretion does not keep up with sea-level rise, the exchange and circulation of Gulf of Mexico and Atlantic water in Florida Bay will increase, shifting the bay from an estuarine to a more marine system and minimizing the influence of any watershed restoration actions. Such increased circulation could also ameliorate the historic effect of the Flagler Railway and Keys Highway, which decreased water exchange between the bay and Atlantic, increased water residence time in the bay, and probably changed circulation and salinity patterns. Finally, with rising sea level, the mangrove shoreline along the northern bay will likely move inland.

Water Quality Responses

Restoration of the Everglades will have effects on the watershed's estuaries beyond changing freshwater input and salinity. Restoration will also affect material (particularly dissolved nutrient) inputs as stormwater treatment areas decrease nutrient inputs to the Everglades (Chimney and Goforth 2001) and changing hydrologic conditions modify biogeochemical cycles and transport within the wetlands. Changing flow and salinity will affect biogeochemical cycling within the estuaries via direct effects of salinity on abiotic processes (e.g., phosphorus sorption-desorption) and indirect effects of changing community structure and associated physical and biogeochemical characteristics (e.g., sediment stabilization and resuspension with changing seagrass cover). The ecological consequences of these changes are uncertain, but one concern is that phytoplankton blooms could be stimulated by Everglades restoration because of potential increases in nitrogen inputs (Brand 2002). Nevertheless, an expectation of Everglades restoration is that such a change in Florida Bay water quality will not occur. Development of a coupled hydrodynamic-water quality model of the bay, combined with monitoring and research of biogeochemical processes will improve understanding and adaptive management responses to this and other aspects of the restoration.

Working Hypotheses: Relationships of Water Quality and External Nutrient Sources. Changing the flow of water through the Everglades and resultant changes in the structure and function of these wetlands will alter the delivery of materials to downstream coastal ecosystems, including Florida Bay. Quantitative predictions of these changes are not possible at this time, but it is reasonable to expect that phosphorus outputs from the Everglades, which are very low, will not change, and nitrogen outputs from the Everglades, which are much greater (Rudnick et al. 1999), could change. Given that most nitrogen output is in the form of dissolved organic matter (DOM), a major uncertainty is the extent to which this DOM can be decomposed by heterotrophic bacteria and phytoplankton and provide nutrients (particularly nitrogen) for phytoplankton. Depending upon the proportion of this bioavailable DOM and the relationship of DOM quality and quantity to freshwater flow, restoration of natural water inflows from the Everglades could affect the composition, magnitude, duration, and distribution of phytoplankton blooms.

Hydrologic restoration of the Everglades could also affect Florida Bay water quality by changing water circulation and water residence time in the bay. Increased freshwater inputs from the Everglades, with lower phosphorus concentrations than in Gulf of Mexico waters, could decrease phosphorus inputs from the Gulf (moving the zone of influence of P-limiting Everglades water westward in the bay) and thus decrease the density and prevalence of *Synechococcus* blooms in central Florida Bay (Boyer and Jones 1999). Furthermore, the magnitude of phytoplankton blooms varies as a function of the residence time of waters within the bay's basins and exchange of these waters with adjacent marine waters. Increased freshwater flow, along with the potential restoration of passes through the Florida Keys, could decrease bay water residence time and phytoplankton blooms.

Working Hypotheses: Relationships of Water Quality and Changing Internal Bay Structure and Function. Everglades restoration will affect Florida Bay water quality via changes in the bay's internal biogeochemical cycles. These internal changes will likely be mediated through changing seagrass community structure and function. An expectation of the restoration is that changing salinity will increase seagrass species diversity and spatial heterogeneity such that large scale *T. testudinum* die-off events will be prevented. In turn, water-quality degradation associated with such events will be prevented. Die-off events can increase phytoplankton growth because of increased sedimentary nutrient mobilization, decreased benthic uptake of nutrients and resultant reduction in competition for water-column nutrients, and decreased grazing pressure from benthic filter feeders (due to loss of their habitat). Sediment resuspension due to seagrass die-off can supply additional water-column nutrients via both porewater advection and desorption of surface-bound nutrients from resuspended particles. The latter process is salinity dependent and will be affected by hydrologic restoration, which may thus influence phosphorus availability for phytoplankton (with lower phosphorus availability as a function of lower salinity).

Nitrogen cycling and availability within the bay are likely to change with restoration, and these internal changes are likely to have greater effects on phytoplankton production than those derived from changing nitrogen inputs from the Everglades. Recent studies found that rapid and variable rates of nitrogen fixation and denitrification occur within bay sediments (particularly benthic microbial mats) and seagrass beds (Nagel 2004, Evans 2005). There is high uncertainty regarding the magnitude of large-scale (space and time), integrated rates of nitrogen cycling, and changes that may occur with restoration.

Seagrass Community and Trophic Web Response

An expectation of Everglades restoration is that changing patterns of freshwater flow toward more natural patterns will drive Florida Bay's seagrass community and trophic web toward its pre-drainage condition.

Working Hypotheses: Multiple Factors Affect the Florida Bay Seagrass Community. Spatial coverage, biomass, production, and taxonomic composition of seagrass beds in Florida Bay are controlled by the combined and inter-related effects of light penetration, epiphyte biomass, nutrient availability, sediment depth, salinity, temperature, sulfide toxicity, and disease. Decreased salinity caused by increasing freshwater flow will have a direct effect on seagrass communities through physiological mechanisms, resulting in greater spatial heterogeneity of seagrass beds, a decrease in the dominance of *T. testudinum*, and an increase in coverage by other seagrass species (*H. wrightii* through much of the bay and *R. maritima* near the northern coast of the bay). Decreased salinity will also decrease the infection of *T. testudinum* by the slime mold, *Labyrinthula*. Light availability will depend upon phytoplankton growth and sediment resuspension, which depend both on nutrient availability, grazing, and stabilization of sediments by seagrass beds.

Working Hypotheses: Changing Salinity and Seagrass Habitat Will Alter Fish Community Structure. Fish and invertebrate species in Florida Bay are expected to be affected by Everglades restoration efforts via responses to changing salinity and habitat. Decreasing salinity, and especially reducing the frequency and duration of hypersaline events, will increase the growth and survival of estuarine species (especially juvenile pink shrimp and juvenile spotted seatrout) and enhance the use of Florida Bay as a nursery. Increased seagrass habitat diversity and heterogeneity (with less area covered by high density *T. testudinum*) and minimizing large-scale *T. testudinum* die-off events will increase the survivorship and population size of these and other higher trophic level species. Both recreational and commercial fisheries are thus expected to benefit from Everglades restoration.

ACKNOWLEDGMENTS

We thank the many scientists and managers who have worked together to develop and explore the concepts that are presented here. This work reflects the collective effort of participants in several workshops and conferences, leading toward a consensus of inference and professional judgment that we present in this paper. In particular, we thank Tom Armentano, Joe Boyer, Larry Brand, Paul Carlson, Mike Durako, Jim Fourqurean, Bob Halley, Gary Hitchock, John Hunt, Bill Kruczynski, Jerry Lorenz, Chris Madden, Doug Morrison, Bill Nuttle, Ed Phlips, Mike Robblee, Darren Rumbold, Tom Schmidt, Steve Traxler, Hal Wanless, and (last, but far from least) Jay Zieman. We also thank Deborah Drum, Shawn Sculley, and anonymous reviewers for review comments, Douglas Wilcox for review and editorial comments, and special thanks to Kim Jacobs for assistance in preparing and initial editing of this paper.

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Manuscript received 28 February 2005; revisions received 14 September 2005; accepted 4 October 2005.

WETLANDS, Vol. 25, No. 4, December 2005, pp. 832–842

A CONCEPTUAL MODEL OF ECOLOGICAL INTERACTIONS IN THE MANGROVE ESTUARIES OF THE FLORIDA EVERGLADES

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Abstract: A brackish water ecotone of coastal bays and lakes, mangrove forests, salt marshes, tidal creeks, and upland hammocks separates Florida Bay, Biscayne Bay, and the Gulf of Mexico from the freshwater Everglades. The Everglades mangrove estuaries are characterized by salinity gradients that vary spatially with topography and vary seasonally and inter-annually with rainfall, tide, and freshwater flow from the Everglades. Because of their location at the lower end of the Everglades drainage basin, Everglades mangrove estuaries have been affected by upstream water management practices that have altered the freshwater heads and flows and that affect salinity gradients. Additionally, interannual variation in precipitation patterns, particularly those caused to El Niño events, control freshwater inputs and salinity dynamics in these estuaries. Two major external drivers on this system are water management activities and global climate change. These drivers lead to two major ecosystem stressors: reduced freshwater flow volume and duration, and sea-level rise. Major ecological attributes include mangrove forest production, soil accretion, and resilience; coastal lake submerged aquatic vegetation; resident mangrove fish populations; wood stork (*Mycteria americana*) and roseate spoonbill (*Platelea ajaja*) nesting colonies; and estuarine crocodilian populations. Causal linkages between stressors and attributes include coastal transgression, hydroperiods, salinity gradients, and the ''white zone'' freshwater/estuarine interface. The functional estuary and its ecological attributes, as influenced by sea level and freshwater flow, must be viewed as spatially dynamic, with a possible near-term balancing of transgression but ultimately a long-term continuation of inland movement. Regardless of the spatio-temporal timing of this transgression, a salinity gradient supportive of ecologically functional Everglades mangrove estuaries will be required to maintain the integrity of the South Florida ecosystem.

Key Words: Everglades, South Florida, ecosystem restoration, conceptual ecological model, mangrove forest, tidal creeks, estuaries, salinity gradients, water management, sea-level rise, estuarine geomorphology, fish communities, wood stork, roseate spoonbill, American crocodile

BACKGROUND

A brackish water ecotone of coastal bays and lakes, mangrove and buttonwood forests, salt marshes, tidal creeks, and upland hammocks separates Florida Bay, southern Biscayne Bay, and the Gulf of Mexico from the freshwater Everglades. The model boundary from Turkey Point west to Lostman's River delineates the interface of Biscayne and Florida Bays and the Gulf of Mexico that is affected by freshwater flows from the Everglades (Figure 1). The Everglades mangrove estuaries are characterized by salinity gradients that vary spatially with topography and seasonally and inter-annually with rainfall, tide, and freshwater flow from the Everglades. Because of their location at the lower end of the Everglades drainage basin, Everglades mangrove estuaries are particularly vulnerable to changes in sea level and freshwater flow.

Everglades mangrove estuaries and their ecological attributes, as influenced by sea-level rise and increased freshwater flow (in both volume and duration), must be viewed as spatially dynamic, with a possible near-term balancing of transgression but ultimately a long-term continuation of inland movement. Regardless of the spatio-temporal timing of this transgression, a salinity gradient supportive of ecologically functional Everglades mangrove estuaries will be required to maintain the integrity of the South Florida ecosystem.

EXTERNAL DRIVERS AND ECOLOGICAL STRESSORS

All ecological processes and attributes in the mangrove coastline of the southern Everglades are hydrologically controlled by sheet flow from the freshwater wetlands to the north interacting with sea level in the Gulf of Mexico and Florida Bay (Figure 2). Responses to changes in freshwater flow from the implementation of CERP are relatively short term in comparison to the longer-term, progressively increasing changes resulting from relative sea-level rise.

Freshwater Flow

Construction and operation of South Florida's water management system during the Twentieth Century has depleted freshwater flow to the Everglades mangrove estuaries and has altered its timing and distribution (McIvor et al. 1994, VanZee 1999). There are numerous examples of how ecological patterns and processes in the mangrove estuaries are closely linked to patterns of hydrology, salinity, and supply of marine-derived phosphorus, all of which have been altered by reduced freshwater flow (Chen and Twilley 1999, Ross et al. 2000). Because the upstream freshwater Everglades system is so oligotrophic and phosphorus-limited (Noe et al. 2001), the ocean is the source of the limiting nutrient to these estuaries. This "upside-down" characteristic of Everglades estuaries is a defining feature and plays a strong role in the interaction of geomorphology and productivity (Childers et al. 2005).

Additionally, Childers et al. (2005) suggested that water residence time, particularly during the dry months, plays a key role in phosphorus cycling in Everglades mangrove estuaries. Along west coast systems, such as Shark River, low freshwater inflows at this time allow salinity incursions up-estuary, extending the influence of the marine phosphorus source to the oligohaline ecotone. In the Florida Bay mangrove zone, though, the loss of freshwater inflow effectively eliminates flushing, and water residence times are long. During this time, Childers et al. (2005) hypothesized that internal recycling of phosphorus (primarily via subtidal and open water processes) and nitrogen (primarily mediated by the mangrove wetlands) dominate dry season dynamics.

Sea-Level Rise

The rate of relative sea-level rise for South Florida increased above recent decadal rates beginning about 1930. Since that time, South Florida has had a relative sea-level rise of about 23 cm (Wanless et al. 1994). This is a rate of 30 cm per century. Anticipated response to global warming is projected to result in a global increase in sea level of about 60 cm in the coming century. Sea-level rise may massively reconfigure geomorphology, circulation patterns, salinity patterns, and ecological processes during the Twenty-First Century (Wanless et al. 1994).

Non-Native Plants and Fishes

The introduction and spread of non-native plants and fishes are additional drivers and stressors on the Everglades mangrove estuaries, although they are not included in this model because of the overwhelming influences of sea level and hydrology. The Mayan cichlid presently dominates the fish community in mangrove wetlands east of Taylor Slough (Trexler et al. 2001), and the non-native plants Brazilian pepper (*Schinus terebinthifolius* Raddi) and common colubrine (*Colubrina asiatica* (L.) Brongn) have invaded mangrove forests. Although less pervasive than sea level and freshwater flow, potential impacts from the spread of non-native plants and fishes merit a better understanding of their ecological roles and potentials for control.

ECOLOGICAL ATTRIBUTES

Mangrove Forest Production, Soil Accretion, and Resilience

Mangrove forests (red mangroves [*Rhizophora mangle* Linnaeus], black mangroves [*Avicennia germinans* (L.) Linnaeus], white mangroves [*Laguncularia racemosa* (L.) Gaertn.f.)], and buttonwood [*Conocarpus erectus*]) dominate primary productivity and soil accretion within the Everglades mangrove estuaries

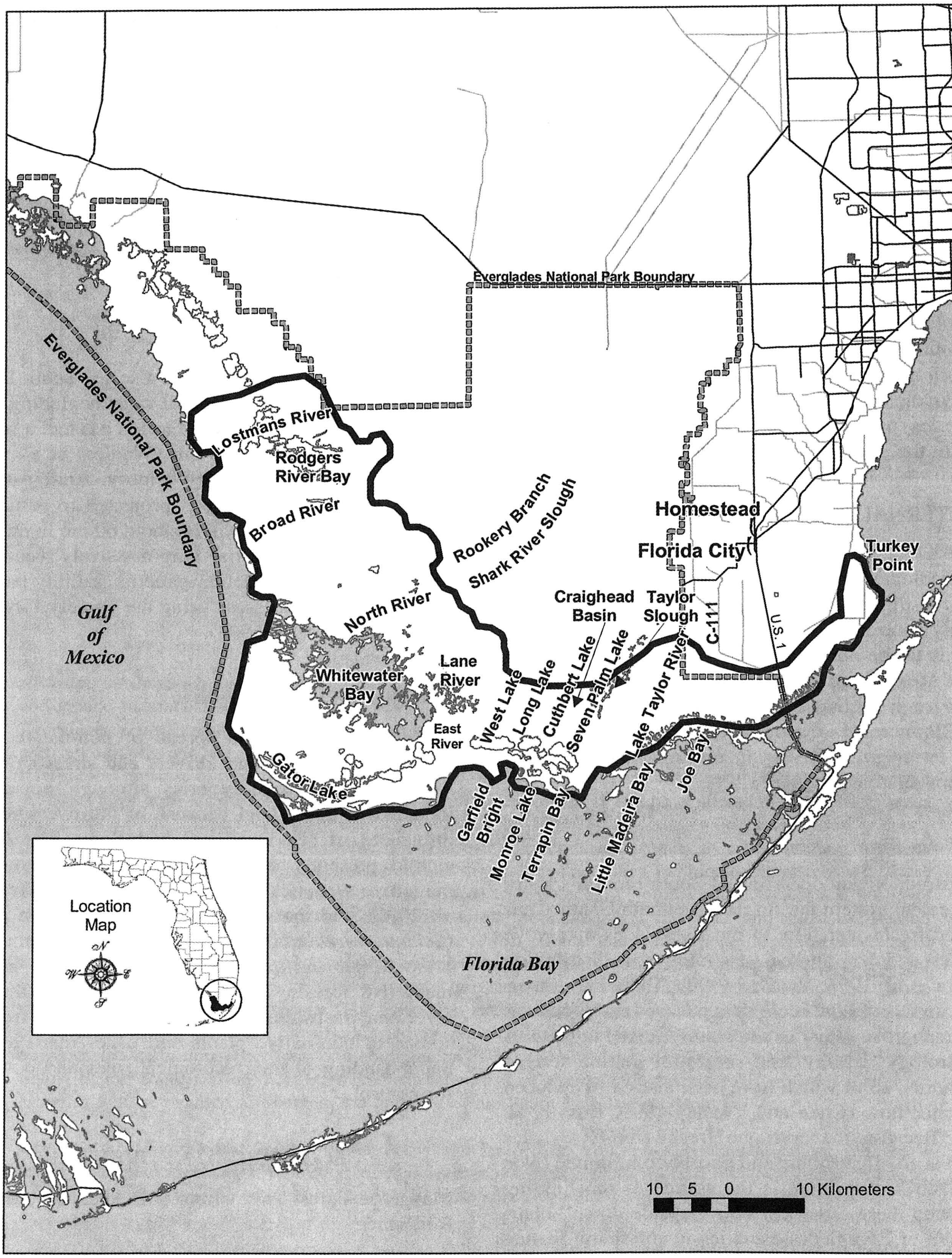

Figure 1. Boundary of the Everglades Mangrove Estuaries Conceptual Ecological Model.

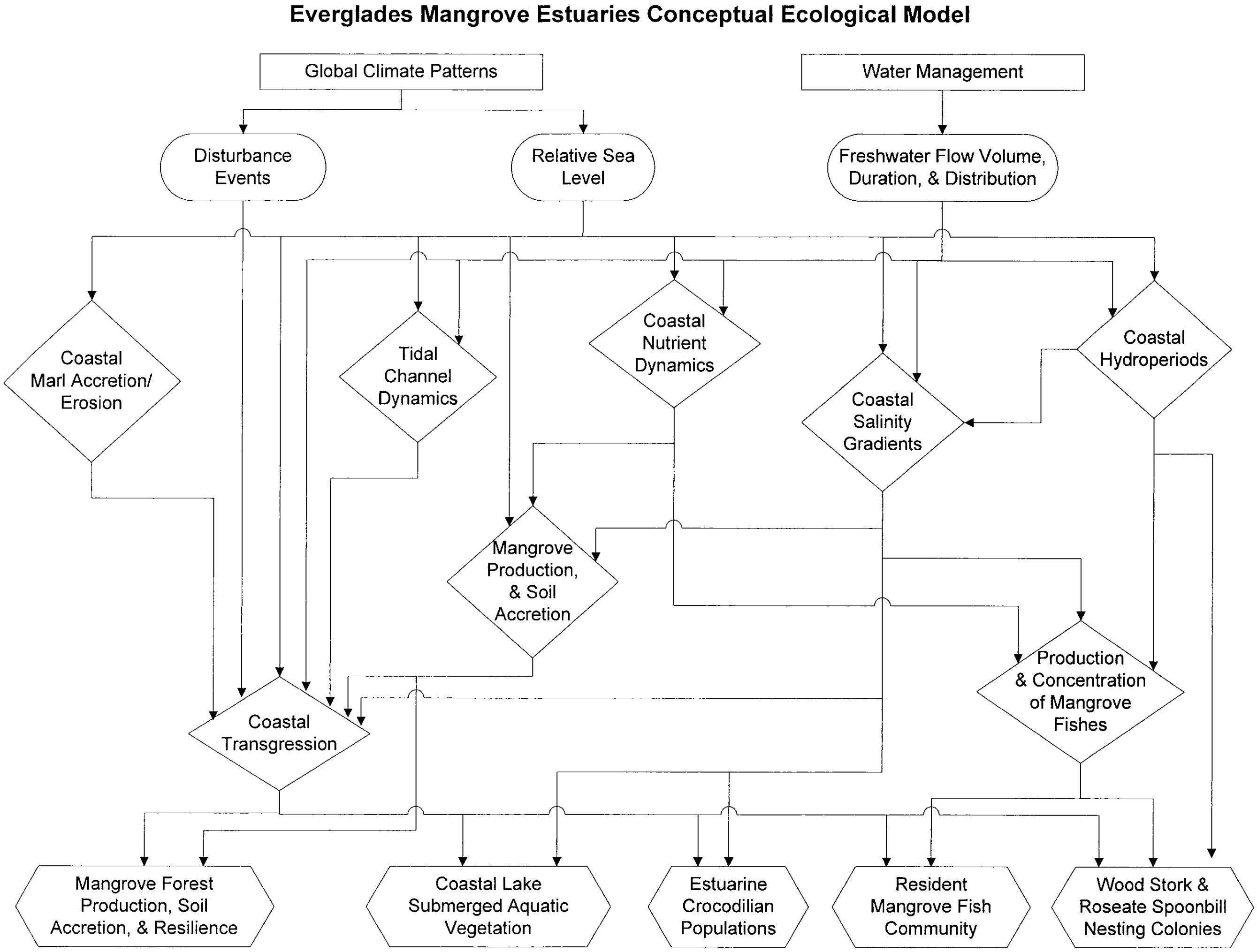

Figure 2. Everglades Mangrove Estuaries Conceptual Ecological Model diagram.

(Twilley 1998, Chen and Twilley 1999, Childers et al. 1999, Davis et al. 2004). That productivity appears to reflect the nutrient status of the estuarine interface, which is related to mixing of phosphorus-poor water from the freshwater Everglades with relatively phosphorus-rich water from the Gulf of Mexico (Davis et al. 2001 a, b, Davis et al. 2003, Childers et al. 2005).

Aboveground biomass and production in the mangrove forests of Shark River Slough and other Gulf estuaries increase from the ecotone toward the Gulf of Mexico, reflecting the direct connection of these systems to the marine phosphorus source (Chen and Twilley 1999, Rudnick et al. 1999, Childers et al. 2005). Trees in the forests near the Gulf are able to allocate more biomass to aboveground growth. The dwarf mangrove forests along the northern margin of Florida Bay reflect suppressed levels of aboveground productivity and seedling development, as influenced by minimal P supply from either the oligotrophic marshes of the southern Everglades or Florida Bay (Koch 1997, Koch and Snedaker 1997, Satula et al. 2003, Childers et al 2005). High belowground production rates in the dwarf mangrove forests appear to be a biomass allocation phenomenon in which mangroves in the oligotrophic southern Everglades are foraging for nutrients (Krauss et al. 2003). The counter-intuitive expectation is that maintenance of oligotrophic conditions in the southern Everglades [by increased freshwater inflows] may promote peat accretion in these mangroves.

Red mangrove forests in South Florida can potentially accrete organic peat substrate at 2–6 mm/year. Disturbances (major hurricanes, fire, freeze, and changing flushing) disrupt that rate and commonly result in phases of substrate subsidence from decay (Smith et al. 1994, Cahoon and Lynch 1997). Nutrient limitation and salinity stress also reduce that rate.

An important feature for maintenance of an existing wetland environment, its recovery following disturbance events such as hurricanes, freezes, fires, or salinity changes, or the successful shift from one wetland type to another is maintenance of good flushing by either fresh or saline waters (Wanless et al. 1995).

Where flow and flushing diminish, wetland communities collapse (Wanless and Vlaswinkel 2005). This is true for long-term maintenance of mangrove communities and for mangrove communities invading former sawgrass wetlands.

Terrestrial communities embedded in the mangrove forests include tropical forest communities and halophytic prairies. Midden forests, thatch palm (*Thrinax* spp.) hammocks, mixed coastal hammocks, and buttonwood hammocks contribute to local and landscape species diversity within the mangrove zone (including providing substrate for epiphytes) and are able to persist because of the presence of elevated substrates like storm berms and human-originated deposits (Craighead and Gilbert 1962, Craighead 1971). Halophytic prairies dominated by *Batis maritima* Linnaeus, *Salicornia* spp., and *Blutaparon vermiculare* (L.) Mears) appear to represent a long-term landscape element that becomes established where tropical storms alter coastal soils in such a way that mangrove and buttonwood forests are killed (Craighead and Gilbert 1962, Craighead 1971, Armentano et al. 1995).

Coastal Lake Submerged Aquatic Vegetation Communities

Coastal lakes such as Seven Palm Lake, Cuthbert Lake, Long Lake, West Lake, Lake Monroe, and the Taylor River ponds support seasonal beds of SAV under oligohaline to mesohaline conditions. Species richness and total and species-specific percent cover of SAV found in the lakes, ponds, and bays that make up this aquatic network vary both seasonally and interannually in patterns that are related to salinity (Morrison and Bean 1997). Salinity ranges for the suite of 10–12 species, including bladderwort (*Utricularia* spp.) and naiads (*Najas* spp.) are well-documented, with an upper limit of approximately 5–8 ppt, muskgrass (*Chara* spp.) under mesohaline salinities of approximately 15–20 ppt, and widgeon grass (*Ruppia maritima* Linnaeus) under mesohaline salinities of 10–25 ppt.

Waterfowl species that once occurred in large numbers in coastal lakes and basins of the mangrove zone (Kushlan et al. 1982) are dependent on SAV as their primary food resource. The local declines of American coot (*Fulica americana* J.F. Gmelin), lesser scaup (*Aythya affinis* Eyton, 1838), American widgeon (*Anas americana* J.F. Gmelin), and white-cheeked pintail (*Anas bahamensis* Linnaeus) correspond to decline in that food resource, despite overall resurgence of populations in other parts of North America. Recent high-rainfall years have witnessed an increase in coot numbers on West Lake to approximately 2,000 during winter 1996–1997 (O.L. Bass, Jr., Everglades National Park, pers. comm.) but not to the population size of approximately 50,000 that over-wintered there until the 1960s (Kushlan et al. 1982).

Resident Mangrove Fish Populations

Oligohaline wetlands of the mangrove estuary support a resident community of small fishes that is functionally important as an intermediate trophic level supporting wading birds and other higher consumers (Lorenz 2000). Density and seasonal concentration of small marsh fishes in the mangrove zone like sheepshead minnows (*Cyprinodon variegatus* Lacepede), sailfin mollies (*Poecilia latipinna* Lesueur), topminnows (*Fundulus chrysotus* Guenther), rainwater killifish (*Lucania parva* Baird and Girard), and sunfish (*Lepomis marginatus* Holbrook) reflect estuarine salinity, nutrient status, hydroperiod, and drying patterns (Lorenz 2000, Trexler and Loftus 2000), all of which are controlled by freshwater flow and sea level.

The resident fish assemblage decreases in density and size distribution when salinity exceeds 5–8 ppt (Lorenz 1997, 1999, 2000). This relationship has been demonstrated for Florida Bay mangrove wetlands, but not for Gulf of Mexico estuaries. Furthermore, salinity is inversely auto-correlated with hydroperiod in Florida Bay mangrove wetlands, and the relative contribution of each of these variables is not known.

Densities of small fishes in Shark River Slough are approximately 50 percent greater at Rookery Branch, near the interface with the Gulf of Mexico, in comparison to more upstream sites (Trexler and Loftus 2000). Greater fish densities at Rookery Branch hypothetically correspond to enhanced nutrient status and productivity in that area (Childers et al. 1999). In contrast, lower fish densities at the estuarine interface of Taylor Slough relative to sites upstream (Lorenz 1999, 2000, Trexler and Loftus 2000) correspond to low nutrient status and productivity there. Receding water levels following an extended annual hydroperiod can concentrate small fishes in Craighead Basin, at the estuarine interface of Taylor Slough, to densities comparable to the estuarine interface of Shark River Slough (Lorenz 2000).

Relationships of fish populations to hydrology in gulf estuaries are unknown. Populations of small marsh fishes in gulf estuaries may respond to hydroperiod and water recession patterns very differently than Everglades marsh fish communities because of more complex topography created by a dendritic pattern of tidal creeks. Tidal creeks may further influence the resident mangrove fish community as corridors for immigration of juveniles of more marine species.

Wood Stork and Roseate Spoonbill Nesting Colonies

Large nesting colonies of wood storks (*Mycteria americana*, Linnaeus) and great egrets (*Ardea alba*, Linnaeus) in the Everglades during the early 1900s were concentrated in Everglades mangrove estuaries (Ogden 1994). East River, Lane River, Rookery Branch, Broad River, and Rodgers River Bay colonies, in the headwaters of the tidal rivers entering the Gulf of Mexico, supported approximately 90 percent of the total nesting population of these and other wading bird species in the Everglades during the period 1931–1946. Additional colonies along the southern mainland of Florida Bay included Gator Lake, Mud Lake, Mud Hole (located east of Gator Lake), Cuthbert Lake, and Madeira Rookery. All of these coastal nesting colonies collapsed during the second half of the Twentieth Century (Ogden 1994). Larger fishes, such as sunfish and topminnows that grow to 10 cm in length, are considered to be particularly important in the diets of wood storks due to their higher vulnerability to capture (Ogden et al. 1978).

A decrease in roseate spoonbill (*Platelea ajaja*, Linnaeus) nesting in northeast Florida Bay and a shift of nesting distribution from eastern to western Florida Bay accompanied the collapse of the wood stork nesting colonies (Powell et al. 1989, Bjork and Powell 1994, Lorenz et al. 2002). Small fishes have been reported to be the primary diet of roseate spoonbills in Florida Bay (Allen 1942, Powell and Bjork 1990, Dumas 2000). Relatively sparse populations of marsh fishes along the estuarine interface of northeast Florida Bay today require very specific wetland drying patterns to concentrate them and make them available in densities adequate to support spoonbill nesting. Lorenz (2000) reported a water-depth threshold of 12 cm, averaged over the 21-day post-hatching period of roseate spoonbills, that is necessary to concentrate the fish prey base in Taylor Slough coastal sites. Water-level recession to 12-cm depth during that period can concentrate normally low fish density in that region to 85 fish per square meter in remaining pockets of water. The 12-cm depth threshold fits well with success or failure of spoonbill nesting in northeast Florida Bay colonies.

Collapse of coastal wood stork and great egret colonies, and of northeast Florida Bay roseate spoonbill colonies, corresponded to construction of the Central and South Florida (C&SF) Project and the resulting reduction of freshwater flow to the estuarine interface compared to Natural Systems Model (NSM) simulations (VanZee 1999).

Estuarine Crocodilian Populations

The American alligator (*Alligator mississippiensis* Daudin) was historically abundant and nested in freshwater mangrove areas of the Everglades (Craighead 1968). Today, nesting is limited, and few juveniles are observed. Salinity is a major factor limiting distribution and abundance of alligators in estuarine habitats (Dunson and Mazzotti 1989, Mazzotti and Dunson 1989). Alligators lose the capacity to we estuarine habitats for feeding, growth, and reproduction when salinity exceeds oligohaline levels (Joanen 1969). When alligators occur in salt water, it is usually to feed, and there is always a freshwater refugium in close proximity (Jacobsen 1983, Tamarack 1988). In a natural experiment in North Carolina, alligators that were exposed to diversion of freshwater flows due to construction of a power plant relocated to the diversion canal to maintain access to fresh water.

Small alligators are especially vulnerable to exposure to salt water. In laboratory experiments, small alligators ceased feeding and should signs of stress when exposed to salinities greater than 10 ppt (Lauren 1985). Alligators do feed and gain mass at 4 ppt (Mazzotti and Dunson 1984). For these reasons, alligators are good indicators of restoring freshwater flows to estuarine systems and the subsequent reestablishment of an extensive freshwater/brackish water zone.

The American crocodile (*Crocodylus acutus* Cuvier) dwells in ponds and creeks of the mangrove estuaries of Florida Bay (Ogden 1976, Mazzotti 1983). American crocodiles are tolerant of a wide salinity range as adults because of their ability to osmoregulate (Mazzotti 1989). Juvenile crocodiles lack this ability (Mazzotti 1989), however, and their growth and survival decrease at salinities exceeding 20 ppt (Mazzotti and Dunson 1984, Mazzotti et al. 1988, Moler 1991). Juvenile crocodiles tend to seek freshwater pockets, such as black mangrove stands, when those choices are available.

ECOLOGICAL EFFECTS: LINKAGES BETWEEN STRESSORS AND ATTRIBUTES

Coastal Transgression

The stability/instability of the shoreline and coastal wetlands in the southern Everglades is manifest through the dynamic interaction of freshwater outflows, sea-level rise, and saline water inflow, the rate of import/export of sediment, and the capability of the sedimentary environment or bio-sedimentary substrate level to respond to changes in water level. In this time of rapidly rising sea level (Wanless et al. 1997), most mangrove communities are presently losing area of coverage (Wanless et al. 2000). In the coming century, the coastal mangrove community can be expected to become increasingly dissected. Sustained rates of accretion of coastal marl shorelines of Florida Bay probably are also incapable of keeping up with predicted rates of sea-level rise, and over-topping and breaching of embankments during storm events are likely under future scenarios of rising sea level.

Where rates of peat or marl elevation buildup do not keep up with rates of sea-level rise, shoreline transgression and landward salinity intrusion will lead to mangrove erosion along shorelines and mangrove movement into interior landscapes. Saline intrusion into freshwater wetlands underlain by peat substrate may lead to wetland collapse and transformation to open, saline ponds and estuaries (Wanless and Vlaswinkel 2005). Saline intrusion into marl substrate wetlands results in an advancing zone of diminished productivity (white zone) (Ross et al. 2002). Restoration of freshwater flow volume, timing, and distribution may slow the inland movement but will not change the rate of erosion along the shoreline.

The coastal Everglades have also been re-configured during the past century by filling in of tidal creeks. Siltation and mangrove encroachment of tidal creeks (Craighead 1971, Meeder et al. 1996) has progressed to the extent that open water courses that were described earlier this century are no longer recognizable (G. Simmons, gladesman, pers. comm.). Reduced freshwater flow volume and rising sea level are probable contributing factors.

Coastal Hydroperiods and Salinity Gradients

Pre-drainage hydrologic conditions in the southern Everglades produced prolonged pooling of freshwater just upstream from the mangrove estuaries and prolonged durations of freshwater flow into the estuaries (VanZee 1999). The freshwater pooling and inflow supported wide salinity gradients, including a broad oligohaline zone, in the mangrove estuaries.

A combination of reduced freshwater flow and increased relative sea-level rise has resulted in higher salinities in the formerly oligohaline mangrove zone and significant saline intrusion into former freshwater marshes of the lower Everglades (Ross et al. 2000, Ross et al. 2002). Although surface-water salinities fluctuate laterally through wet and dry seasons, saline ground-water intrusion has moved and remains far inland of the position prior to drainage.

White Zone

At the landward interface of the mangrove estuaries with marl wetlands, a ''white zone'' band of sparse, mixed mangrove and graminoid vegetation that appears white on color infrared or black-and-white aerial photos. As with any upper bound on an oligohaline ectone, this zone integrates the balance between freshwater flow and sea-level rise (Ross et al. 2002). Egler (1952) described the white zone as a band of low, open vegetation separating mangrove swamps adjacent to the southeast saline Everglades coast (Taylor Slough to Turkey Point) from sawgrass marshes of the interior. Its composition included a mixture of sawgrass (*Cladium jamaicense* Crantz), spikerush (*Eleocharis* spp.), and red mangrove. He considered the inner edge to mark the farthest extent of storm tides. Ross et al. (2000) documented changes in extent and plant species composition of the white zone since Eglers work. They found movement toward the interior of less than 1 km up to about 4 km throughout the region over about 50 years. Movement was maximal in areas where virtually all freshwater has been blocked by canals and management (wetlands east of US 1), and minimal in wetlands where water flow was less impacted by canals, levees, and management (wetlands west of US 1 and directly south of the C-111 Canal). These patterns suggest that freshwater inflows [at least] partially counteract transgression driven by sea-level rise. Working along a hydrologically isolated coastal transect south of Turkey Point, Meeder et al. (1996) documented an inland movement of the interior boundary of the white zone of 1.9 km during 1940–1994. This distance equated to a vertical shift of 13 cm during a period in which sea level rose by only 11 cm.

WORKING HYPOTHESES FOR RESTORATION

Coastal Transgression

Sustained buildup of substrate by physical and biological processes in many coastal marl and mangrove environments of South Florida will not be capable of keeping up with rates of sea-level rise during the twenty-first century. Where rates of peat or marl elevation do not keep up with rates of sea-level rise, shoreline transgression and landward salinity intrusion into mangrove and freshwater wetlands will occur.

White Zone

If sea level continues to rise at its current rate or faster, the leading edge of the white zone will continue to move toward the interior, except along tidal creeks or major drainages. These changes will be least evident in areas in which freshwater input is augmented and greatest in areas cut off from freshwater flow.

Coastal Tidal Channel Characteristics

The dendritic pattern, channel width and depth, flow volume, and material transport of tidal watercourses through the coastal mangrove estuaries are controlled by sea level interacting with the volume, timing, and distribution of sheet flow and channel flow from the southern Everglades. Many tidal creeks through coastal wetlands of the Everglades have disappeared entirely during the past century because they have been filled in with sediments and with the vegetation of surrounding landscapes. Reduced freshwater flow volume and rising sea level are probable contributing factors. Restored freshwater inflow from the Everglades is expected to help sustain open watercourses through the estuary that will more closely resemble historic patterns, yet sea-level rise is expected to modify the patterns of connectivity through the coastal wetlands and create increased sediment loads.

Coastal Hydroperiod and Depth Patterns

Sheet flow in the southern Everglades prior to drainage produced persistent pooling of fresh water upstream from the mangrove estuaries and prolonged freshwater flow into the mangrove estuaries. Reduced volume and duration of freshwater flow have shortened hydroperiods in the southern Everglades, disrupted in sheet flow, and reduced duration of pooling along the sawgrass/mangrove ecotone. Restoration of pre-drainage volume, distribution, and duration of sheet flow in the southern Evergladeds will prolong pooling of fresh water along the sawgrass/mangrove interface and increase volumes and durations of freshwater flow to the estuaries.

Coastal Salinity Gradients

Prolonged pooling of fresh water upstream of the mangrove estuaries and prolonged patterns of freshwater flow supported a wide salinity gradient, including a broad oligohaline zone, in the mangrove estuary. A combination of historical reduced freshwater flow and increased relative sea-level rise have resulted in higher salinities in the formally estuarine mangrove zone and significant saline intrusion into former freshwater marshes of the lower Everglades. Increasing seasonal freshwater sheet flow to the lower Everglades is expected to provide a broader zone of salinity gradients in the lower Everglades and coastal wetlands and should, in the short term, re-establish an oligohaline zone in the coastal wetlands. Over a long-term period, rising sea level is expected to result in high tides overtopping coastal marl ridges and saline waters penetrating more deeply through tidal channels and mangrove forests, shifting the areas of fresh and lower salinity waters inland.

Production and Organic Soil Accretion of Coastal Mangrove Forests

Production and organic soil accretion in the mangrove forests of the coastal Everglades are controlled by phosphorus availability, with relatively large inputs from marine sources and small inputs from freshwater sources. Increased freshwater sheet flow caused by implementation of CERP projects is expected to maintain low nutrient conditions in the southern Everglades mangrove estuaries and in the oligohaline ecotone forests of the western mangrove estuaries. Low nutrient conditions are expected to enhance belowground productivity by mangroves, which will maintain peat production and soil elevation increases—ultimately enhancing the ability of these low salinity forests to maintain themselves against sea-level rise.

Resilience of Coastal Mangrove Forests

Resilience of the mangrove forests of the coastal Everglades after disturbance is dependent on hydrologic flushing by either fresh or saline water, which is driven by sea level and sheet flow from the Everglades. Resilience also varies with soil fertility. Improved freshwater flow and flushing through the lower Everglades and coastal wetlands (through both channel and sheet flow) are expected to aid in recovery of wetlands from catastrophic setbacks (from hurricanes, fire, freeze, and salinity changes).

Coastal Lake Submerged Aquatic Vegetation and Waterfowl

Prolonged periods of elevated salinity in coastal lakes and basins, resulting from diminished freshwater flow volume and duration, have reduced seasonal duration and cover of communities of SAV along shorelines and in tributaries. SAV communities will persist in larger beds, longer into the dry season, and lower in the estuarine system when oligohaline to mesohaline conditions are restored upon resumption of natural freshwater flow volume and duration.

Resident Mangrove Fish Populations

The wet-season density, size structure, and relative abundance of resident mangrove fish populations are directly related to the time since the last dry-down, the length of time the marsh was dry, and salinity in coastal ecotones. Responses of fishes are non-linear and species-specific. The concentration of resident mangrove fishes into high-density patches where wading birds can feed effectively is controlled by the rate of dry-season water-level recession and local topography/

habitat heterogeneity. Restoration of persistent pools of fresh-to-oligohaline water along the interface where mangrove forests meet the Everglades will support increased densities, size distributions, and seasonal concentrations of resident mangrove fishes due to combined effects of prolonged hydroperiod, enhanced drying patterns, and extended periods of freshwater to oligohaline salinity.

Wood Stork and Roseate Spoonbill Nesting Colonies

The collapse of coastal wood stork and great egret nesting colonies in the tributary headwaters and southern mainland of the Everglades mangrove estuary, and the abandonment of roseate spoonbill nesting colonies in islands of northeast Florida Bay, are attributed to declines in population densities and seasonal concentrations of marsh fishes and other wading bird prey in the southern Everglades. Restoration of densities and seasonal concentrations of resident mangrove fishes in persistent pools of fresh-to-oligohaline water immediately upstream from the mangrove forests will provide the necessary prey base in juxtaposition to nesting habitats to re-establish coastal nesting colonies of wood stork and great egret and northeast Florida Bay nesting colonies of roseate spoonbill.

American Alligator

American alligator distribution, abundance, reproduction, and body condition in the Everglades mangrove estuaries are controlled by salinity. Reduced freshwater flow into the mangrove estuaries of the southern Everglades has resulted in succession of former freshwater mangrove areas to saltwater systems, reducing American alligator populations in tidal rivers and tributaries. With the resumption of natural patterns of volume, timing, and distribution of flow to the Everglades, the American alligator is expected to repopulate and resume nesting in the freshwater reaches of tidal rivers in the mangrove estuaries.

American Crocodile

American crocodile relative density and juvenile growth, survival, and condition increase when salinity fluctuates below 20 ppt in shoreline, pond, and creek habitats in Everglades mangrove estuaries. Alteration of location and quantity of freshwater flow to the mangrove estuaries has lowered the relative density of crocodiles in areas where freshwater has been diverted and decreased growth and survival of juvenile crocodiles throughout the estuary in areas of higher salinities. Restoration of Volume, timing, and distribution of freshwater flow will result in an increase in relative density of crocodiles in areas of restored flow, such as Taylor Slough/Taylor River drainage. Reestablishing the salinity gradient in the estuary will increase growth and survival of juvenile crocodiles throughout the estuary.

ACKNOWLEDGMENTS

We gratefully acknowledge the following individuals who participated in workshops leading to the development of the Everglades Mangrove Estuaries Conceptual Model: Tom Armentano, Tom Bancroft, Tomma Barnes, Sonny Bass, Laura Brandt, Joan Browder, Gwen Burzycki, Evan Chipouras, Craig Faunce, Peter Frederick, Dale Gawlik, Lee Hefty, Lorraine Heisler, Marguerite Koch, Bill Loftus, Frank Mazzotti, Linda McCarthy, Heather McSherry, Doug Morrison, Jon Moulding, Bill Nuttle, John Ogden, Robert Pace, Sue Perry, Mary Ann Poole, Mike Robblee, Bill Robertson, Mike Ross, David Rudnick, Tom Schmidt, Fred Sklar, Tom Smith, Sam Snedaker, Skip Snow, Tim Towles, Steve Traxler, Joel Trexler, Dewey Worth, and Elizabeth Zenker. Partial support was provided to Dan Childers for conceptual model development and for preparation of this manuscript by the National Science Foundation through the Florida Coastal Everglades LTER Program (DEB-9910514). We particularly thank Dr. Jack Gentile for facilitating the initiation of conceptual models for South Florida ecosystem restoration and for informing the conceptual model teams of the process for conceptual model development.

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Manuscript received 28 February 2005; revisions received 13 September 2005; accepted 3 October 2005.